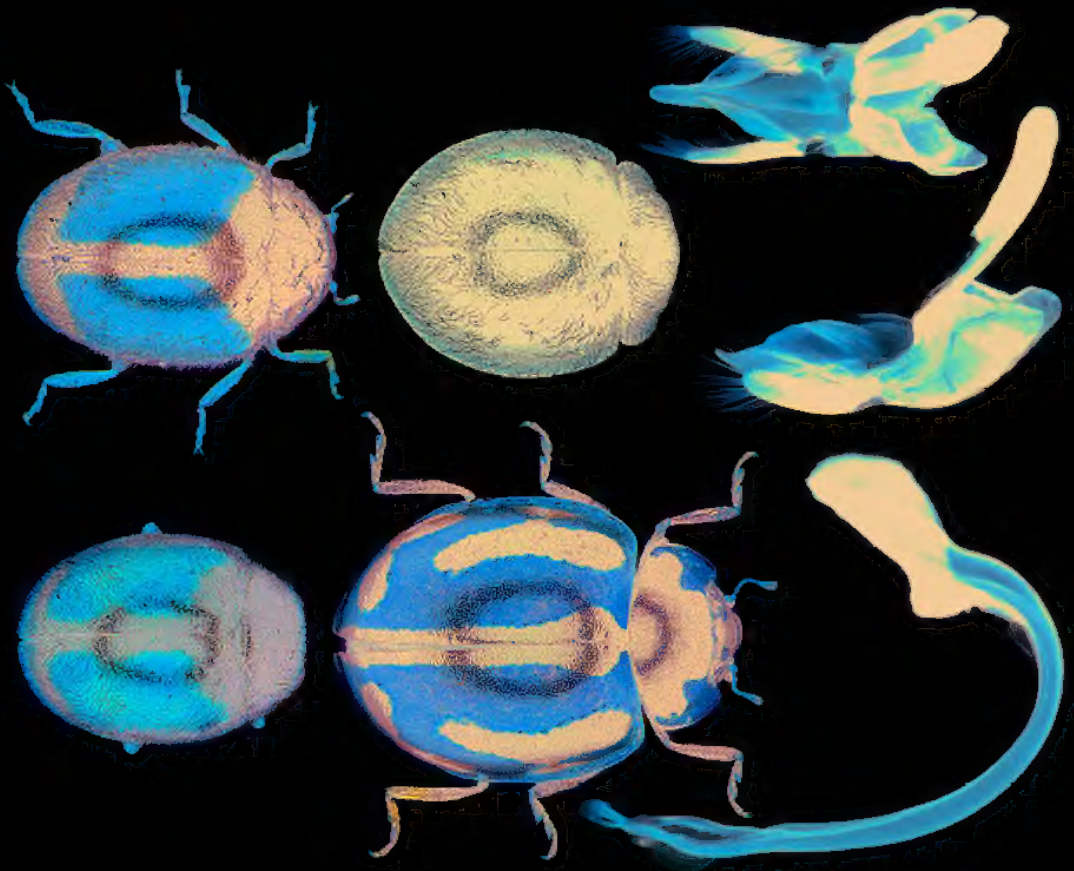


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Research article[urn:lsid:zoobank.org:pub:9202B13C-4294-4049-8DEB-42534205BDF5](https://zoobank.org/pub:9202B13C-4294-4049-8DEB-42534205BDF5)**A new species of fan-throated lizard of the genus *Sitana* Cuvier, 1829
(Squamata: Agamidae) from northern Karnataka, India****Mayuresh Ambekar¹, Arya Murthy² & Zeeshan A. Mirza^{3,*}**^{1,3}*National Centre for Biological Sciences, Tata Institute for Fundamental Research, Bangalore, Karnataka 560065, India*²*Inventure Academy, Whitefield, Sarjapur Road, Bangalore, Karnataka 562125, India***Corresponding author: Email: snakeszeeshan@gmail.com*¹[urn:lsid:zoobank.org:author:3714B65D-DE0A-4C38-A054-B0B7EFECCF8B](https://zoobank.org/author:3714B65D-DE0A-4C38-A054-B0B7EFECCF8B)²[urn:lsid:zoobank.org:author:25DD6BF3-5EC4-40A3-ACD4-915638D4BF47](https://zoobank.org/author:25DD6BF3-5EC4-40A3-ACD4-915638D4BF47)³[urn:lsid:zoobank.org:author:25F673F0-3FB9-4A4F-81CE-997748CC26E6](https://zoobank.org/author:25F673F0-3FB9-4A4F-81CE-997748CC26E6)

Abstract. A new species of fan-throated lizard of the genus *Sitana* Cuvier, 1829 is described from northern Karnataka, India. The new species is similar to members of the clade of *Sitana spinaecephalus* Deepak et al., 2016, however, can be distinguished based on morphological as well as molecular data. *Sitana dharwarensis* sp. nov. differs from its sister species, *S. laticeps* Deepak & Giri, 2016 in bearing a much larger dewlap. Data from micro-CT scan of the cranium and jaws further add support to the distinctness of the new species. The rivers, namely Krishna and Tungabhadra, likely act as a biogeographic barrier for terrestrial lizard species.

Key words. Reptilia, mtDNA, molecular phylogeny, micro-CT scan, taxonomy.

INTRODUCTION

Members of the genus *Sitana* Cuvier, 1829 have received considerable attention from the view of systematics, evident from the recent surge in species descriptions in the last five years (Amarasinghe et al. 2015; Deepak et al. 2016a; b; Deepak & Karanth 2017; Sadasivan et al. 2018). The genus currently contains eleven species, however, a recent molecular investigation hints at the presence of additional undescribed species (Deepak & Karanth 2017).

During the course of a herpetological investigation trip to northern Karnataka, a state in south India, we collected specimens of *Sitana*, which resembled *S. laticeps* Deepak & Giri, 2016, and *S. spinaecephalus* Deepak, Vyas & Giri, 2016 based on the dewlap coloration (Deepak et al. 2016a). Molecular data for a specimen was generated which shows that the specimen was genetically related to *S. laticeps*, however, it differed in several aspects with regard to its morphology. Phylogenetic analysis based on existing sequences generated by Deepak & Karanth (Deepak & Karanth 2017) and the sequence generated in the present work recovered two well supported clades; one representing *S. laticeps sensu stricto* occurring north of Krishna river, and a second clade representing specimens from south of the river. The clade containing sequences from south of Krishna river is divergent and exhibits unique set of morphological characters which enables us to describe it as a new species herein based on

molecular as well as morphological data, further supported by its allopatric range.

MATERIALS AND METHODS

Morphology. Specimens were collected by hand, euthanized and fixed in 6% formalin. They were later washed and stored in 70% ethanol. Muscle tissue was taken prior to fixation and stored for molecular work. The type specimens are deposited in the collection of the Bombay National History Society, Mumbai (BNHS) and the collection facility of the National Centre for Biological Sciences, Bangalore (NCBS). Specimens were measured using a MitutoyoTM digital caliper. Descriptive style and morphometric/morphological characteristics were recorded as follows (Sadasivan et al. 2018). The following measurements were taken: snout-vent length (SVL, from tip of snout to anterior border of cloaca), head length (HL, from snout tip to posterior border of tympanum), head width (HW, distance from left to right outer edge of the head at its widest point), head height (HH, dorsoventral distance from top of head to underside of jaw at transverse plane intersecting angle of jaws), snout-eye length (SE, from snout tip to anterior border of orbit), eye to tympanum (ET, from posterior border of orbit to anterior border of tympanum), jaw length (JL, from rostrum to corner of jaw), interorbital width (IO, transverse distance between anterodorsal corners of left and right

orbits), nares to eye (NE, distance from the anterior edge of orbit to posterior edge of naris), snout width/internasal distance (IN, transverse distance between left and right nares), tympanum diameter (TD, greatest diameter of tympanum), orbit diameter (OD, distance between anterior and posterior margins of orbit), lower arm length (LAL, distance from elbow to distal end of wrist, or just underside of forefoot when the limb is flexed), upper arm length (UAL, distance from anterior insertion of forelimb to elbow when the limb is flexed), finger lengths (F1, F2, F3, F4, F5) (e.g., F4 = Distance from juncture of 3rd and 4th digits to distalmost extent of 4th finger including the claw), femur length (FEL, length of femur from groin to knee), crus length (CL, length of crus (tibia) from knee to heel), hind foot length (HFL, distance from proximal end (heel) of hind foot to distal most point of fourth toe), hind limb length (HLL, from groin to tip of fourth toe), toe lengths (T1, T2, T3, T4) (e.g., T4 = Distance from juncture of 3rd and 4th digits to distal end of 4th digit on hind foot), trunk length (TrL, from forelimb insertion to hind limb insertion), trunk height (TrH, depth midway between the fore and hind limb insertions), trunk width (TrW, width midway between the fore and hind limb insertions), tail length (TL, from posterior border of cloacal opening to tip of tail), tail height (TH) and tail width (TW, at tail base), dewlap length (DWL, distance between posterior end of dewlap and tip of lower jaw), and extent of dewlap in trunk (DWLT, measured from the axilla till the end of the dewlap). Meristic characters were counted for multiple individuals per species. The following characters were scored: mid-body scale rows (MBS, number of scale rows around the trunk at midbody), ventral scales (VEN, number of scales from below mental around the base of the dewlap to anterior border of cloaca), fourth toe lamellae (LAM4, number of 4th toe lamellae, from 1st lamella at the digit's cleft to the most distal lamella), dewlap scales (ESD, number of enlarged scale rows on the dewlap), supralabials (SL, posterior end defined by the last enlarged scale that contacts the infralabials at the corner of mouth), infralabials (IL, posterior end defined by the posterior most enlarged scales that contact the supralabials at the corner of the mouth), ventral scales on the belly (VENB, number of scales posterior to the dewlap to the anterior border of cloaca), and vertebral scales (VS, number of scales above the vertebral column counted from the mid-dorsal first nuchal spine to a level directly above the cloacal opening).

Institutional abbreviations

NCBS = National Centre for Biological Sciences,
Bangalore
BNHS = Bombay Natural History Society, Mumbai
CES = Centre for Ecological Sciences, Bangalore

Micro-CT scans were generated for three male specimens using a Bruker® Skyscan 1272 (Bruker BioSpin Corporation, Billerica, Massachusetts, USA). Head of the specimens were scanned from 16 to 20 minutes at 15µm. Volume rendering was performed with CTVox (Bruker BioSpin Corporation, Billerica, Massachusetts, USA) and images were edited in Adobe Photoshop CS6. Osteological description is based on volume renders retrieved from CTVox following terminology of the skull described by Evans (Evans 2008).

Molecular analysis: Genomic DNA was extracted from liver tissue following Qiagen DNeasy™ Tissue kits following protocols specified by manufacturers. We amplified partial segment of mitochondrial Nicotinamide Adenine Dinucleotide Dehydrogenase Subunit 2 (*NADH* 2) gene with published primers L4437 5'-AAGCTTTC-GGGCCCATAACC-3' and H5540 5'-TTTAGGGCTTT-GAAGGC-3' (Macey et al. 1997). A 12µl reaction was set containing 5µl of Qiagen Taq PCR Master Mix, 4µl of water, 0.5µl of each primer and 2µl template DNA, carried out with an Eppendorf Mastercycler Nexus GSX1. Thermo-cycle profile used for amplification were as follows: 94°C for 15 minutes, (denaturation temperature 94°C for 50 seconds, annealing temperature 59°C for 50 seconds, elongation temperature 72°C for 1 minutes) x 35 cycles, 72°C for 12 minutes, hold at 4°C. PCR product was cleaned using QIAquick PCR Purification Kit and sequenced with a 3730 DNA Analyzer. Sequences were cleaned and edited in Geneious R6 v.6.18. (Kearse et al. 2012) and were also manually checked in MEGA6. Taxon selection for phylogenetic analysis and additional sequences for the nuclear gene G protein-coupled receptor 149 (R35) were taken from Deepak et al. (2017, 2018). Sequences were aligned with ClustalW (Thompson & Gibson 2002) in MEGA6 (Tamura et al. 2013). Aligned data comprised of 856 bp of ND2 and 649 bp of R35 gene which was analyzed with PartitionFinder (Lanfear et al. 2012) for optimal partitioning strategy and evolutionary substitution model. Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were employed to infer phylogenetic relationships in RAxML (Stamatakis 2014) and MrBayes 3.2.2. (Ronquist & Huelsenbeck 2003) respectively with data partitioned by codon positions. ML analysis was run for 1000 bootstrap replicates under GTR + G model to assess clade support. BI was run for 10 million generations with a sampling rate of 1000 under GTR + G. The analysis was terminated after the standard split frequency reached below 0.05. GenBank accession numbers for the sequence generated of the holotype is MH399850. GenBank accession numbers for sequences used in the present study are listed in supporting material.

RESULTS

Molecular phylogenetics based on a fragment of mitochondrial *ND2* and nuclear *R35* gene recovered *Sitana* specimens from northern Karnataka embedded within a clade containing *S. laticeps* and *S. spinaecephalus* and as the sister taxon to *S. laticeps* with high support from ML (bootstrap 100) & BI (posterior probability 1.0). Among the 856 sites of *ND2* gene, 750 sites are conserved, 106 are variable and 40 parsimony informative sites. Morphological data (see diagnosis below) and molecular data support recognition of the population of *Sitana* from northern Karnataka as a distinct species, which is described here.

Sitana dharwarensis sp. nov.

Sitana laticeps Deepak & Karanth 2018: 56–57 (in part)
Figs 1–4, Table 1

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Holotype. ♂ adult (NCBS-AL142); India, Karnataka, Bagalkot; 16.139744° N, 75.672671° E; alt. 590 m; 14 Apr. 2018; M. Ambekar, A. Murthy & Z. Mirza leg.

Paratypes. 2 ♀♀ adult (BNHS 2510, NCBS-AL143); 1 ♂ adult (BNHS 2509); same data as for holotype.

Diagnosis. *Sitana dharwarensis* sp. nov. is a large sized species in relation to members of the *Sitana spinaecephalus* clade, males reaching SVL of 52 mm. Dewlap large, coloration in breeding males cream to off-white, extending up to 47% of the trunk. Parietal bone with a subtle indentation on the anterior border, maxillary bone short in its length and covers a smaller area of the snout, squamosal long and slender gradually tapering at both ends in a sharp tip and, quadrate robust and stout.

Sitana dharwarensis sp. nov. differs from most known species within the genera *Sitana* and *Sarada* Deepak et al., 2016 in bearing a white colored moderately large dewlap (vs. dewlap in shades of red, blue and black in *Sarada* spp., *Sitana visiri* Deepak, 2016, *S. attenboroughii* Sadasivan et al., 2018, *S. marudhamneydhal* Deepak et al., 2016, *S. bahiri* Amarasinghem et al. 2015, *S. devakai* Amarasinghe et al., 2015). The new species is similar to *S. laticeps* and *S. spinaecephalus* in sharing a white dewlap. It differs from *S. laticeps* in bearing a much larger dewlap, dewlap extending to about 47% of

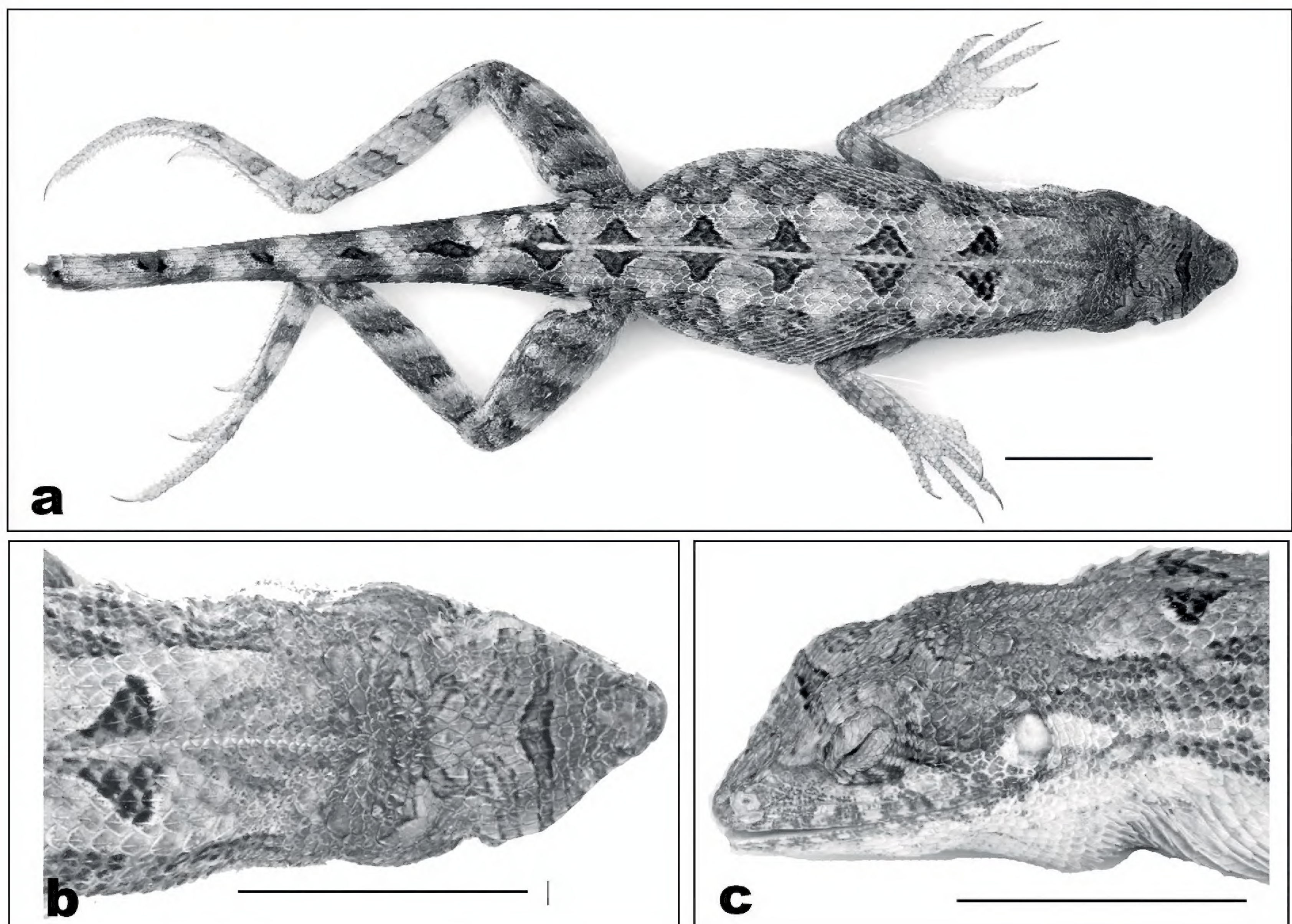


Fig. 1. *Sitana dharwarensis* sp. nov., holotype, ♂ (NCBS-AL142). **a.** Dorsal view of the specimen. **b.** Dorsal view of head. **c.** Lateral view of head. Scale bar: 10 mm.

Table 1. Measurements and morphological details of type specimens of *Sitana dharwarensis* sp. nov. in millimeters

	Holotype NCBS- AL142	Paratype BNHS 2509	Paratype NCBS- AL143	Paratype BNHS 2510
Sex	Male	Male	Female	Female
SVL	52.1	44.8	42.0	39.8
HL	14.1	13.2	12.4	12.2
HW	10.2	9.3	9.1	8.9
HH	9.5	8.2	6.7	7.0
SE	5.5	5.2	5.0	4.8
ET	3.6	3.3	3.1	3.0
JL	15.4	13.9	12.6	12.5
IO	8.0	7.3	6.8	6.6
NE	3.5	2.8	2.6	2.5
IN	2.9	1.9	2.4	2.4
TD	2.1	1.5	1.6	1.5
OD	3.3	2.8	2.9	2.6
LAL	8.5	6.7	6.7	6.4
UAL	10.7	6.6	6.4	6.3
F1	2.0	1.5	1.5	1.5
F2	3.1	2.5	2.5	2.5
F3	4.8	4.0	4.0	3.6
F4	4.5	3.8	3.6	3.3
F5	2.9	2.6	2.3	2.2
FEL	15.7	13.0	12.5	11.7
CL	19.6	15.8	16.6	14.6
HFL	21.9	19.5	19.2	18.0
T1	2.0	1.7	1.6	1.4
T2	3.0	2.8	2.8	2.6
T3	6.0	5.0	4.9	4.9
T4	12.2	10.0	9.2	9.1
TrL	21.3	19.4	19.0	18.8
TrH	9.7	7.5	6.9	6.0
TrW	14.2	12.9	12.6	10.6
TL	-	118.5	112.4	-
TH	4.0	3.1	2.7	2.7
TW	5.4	3.8	3.4	2.9
DWL	33	27.9	—	—
DWLT	9.9	6.9	—	—

the trunk (vs. 29% in *S. laticeps*, 45% in *S. spinaecephalus*). *Sitana dharwarensis* sp. nov. further differs from

S. laticeps in bearing a subtle indentation on the anterior border of parietal (vs. a deep indentation in *S. laticeps*, Fig. 2), the maxillary bone is short and covers a smaller area of the snout (vs. much longer and covering a larger area of the snout in *S. laticeps*), the squamosal is long and slender gradually tapering at both ends in a sharp tip (vs. squamosal short, abruptly ending in a blunt tip at both ends), quadrate is robust and stout (vs. slender in *S. laticeps*, Fig. 2).

Genetic divergence. Genetic divergence (un-corrected p-distance) between populations of *S. dharwarensis* sp. nov. was 1–2% whereas it was 3–4% from *S. laticeps*.

Description. The holotype male (NCBS-AL142) is in generally good condition, with an incision on the thigh made to remove muscle tissue. The entire tail is broken from its base and is preserved separately.

Adult male SVL 52.8 mm. Head relatively long (HL/SVL ratio 0.27), wide (HW/HL ratio 0.72), not depressed (HH/HL ratio 0.67), distinct from neck (Fig. 1a). Snout moderately long (SE/HL ratio 0.39) bluntly conical; longer than eye diameter (OD/SE ratio 0.45) (Fig. 1c). Eye large (OD/HL ratio 0.56); pupil round, eyelids covered with small pentagonal and hexagonal scales, supraciliaries short. Snout obtusely pointed when viewed dorsally, rostral much wider than deep, bordered posteriorly by two supralabials, prenasal and dorsally by three small scales. Canthus rostralis and supraciliary edge moderately sharp consisting of nine scales. Nostrils positioned in the centre of a large, undivided nasal plate, bordered by eight scales (right side), including one prenasal, two postnasals and one supranasal, and separated from rostral by prenasal and supralabials. Ten rectangular, weakly keeled supralabials, bordered above by a single row of slightly smaller, rectangular, keeled scales. Loreal region concave, scales of the loreal region heterogeneous in size, flat, keeled, some roughly hexagonal. Scales on postorbital and temporal region homogenous, imbricate, strongly keeled, and directed posteriorly and dorsally. Orbital scales small but not granular. Tympanum naked. Canthals enlarged, overlapping, becoming slightly smaller along subimbricate supraciliaries, protruding slightly laterally on supraorbital ridge. Scales on dorsal surface of snout, forehead, interorbital, and occipital region heterogeneous in size, and shape; mostly elongate, imbricate, strongly keeled longitudinally; those on snout smaller, rhomboidal, those on forehead largest, greatly elongate; supraorbital scales increase in size becoming more elongate from supraciliaries to inner edges of orbits, of which the enlarged scales follow the curvature of the orbit posterolaterally; occipital region with slightly smaller, less elongate; imbricate, and keeled scales. Parietal plate with pineal eye, the plate slightly larger than adjacent scales. Mental shield narrower than rostral; gular scales keeled. Dewlap moderately large, extends posteriorly over 47%

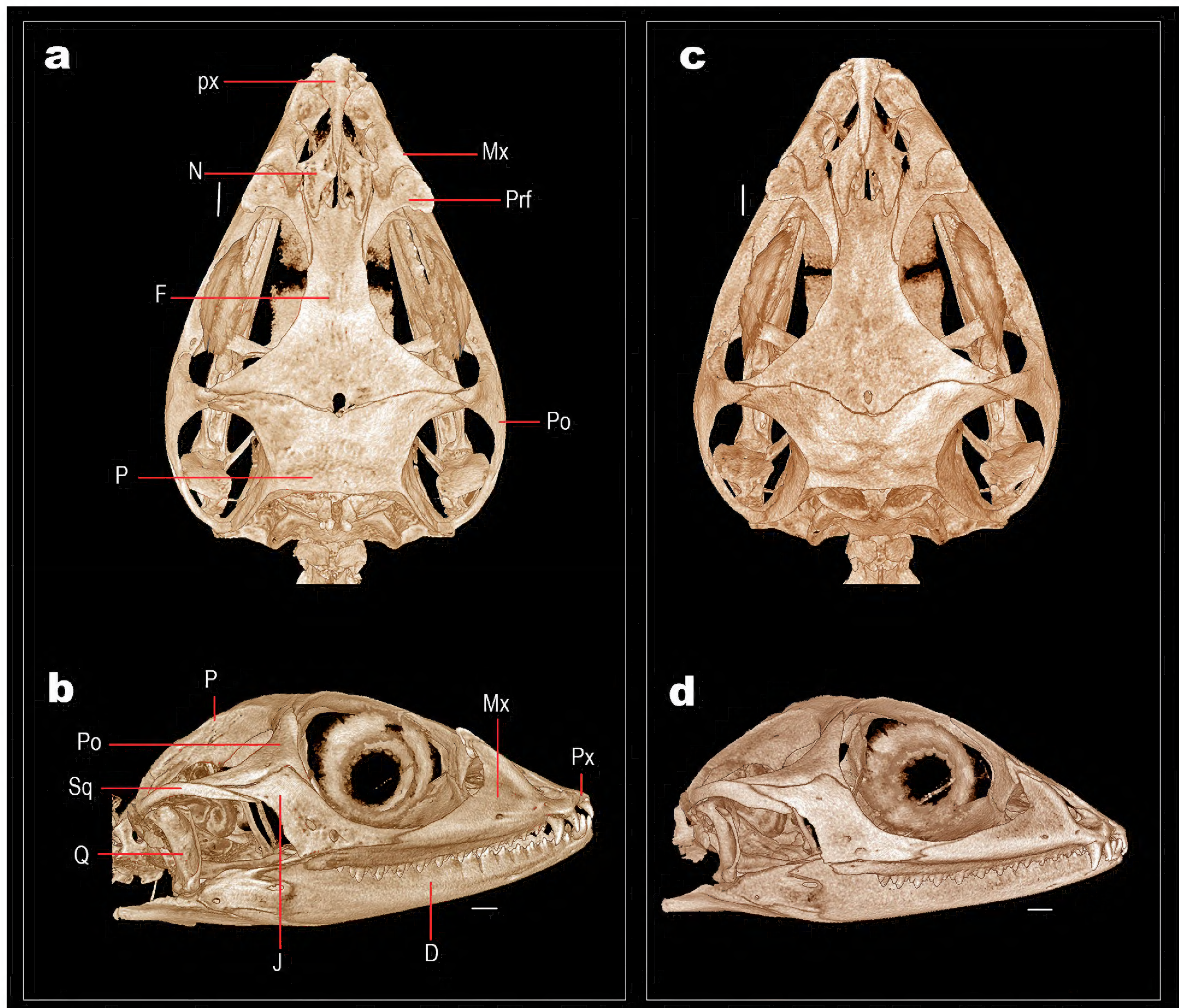


Fig. 2. Micro-CT scan image of the cranium and jaws of *Sitana dharwarensis* sp. nov. (a–b) and *Sitana laticeps* (c–d). **a, c.** Dorsal view of skull. **b, d.** Lateral view. Scale bar: 1 mm. Abbreviations: D = dentary, F = frontal, J = jugal, Mx = maxilla, N = nasal, parietal, Po = postorbital, prf = prefrontal, Px = premaxilla, Q = quadrate, Sq = squamosal (Evans 2008).

of trunk length, with posterior scales extending slightly beyond axila, not extending to mid-venter, approximately four to five rows of anteriodorsal dewlap scales smaller, elongate, pointed, keeled, remainder of scales much larger, keeled, lanceolate, bluntly pointed, gradually increasing in size towards margin, single marginal row largest with many more pointed scales. 17 enlarged rows of scales on dewlap. Nuchal and dorsal crest absent. Scales on nuchal region smaller, less than half the size of those on interorbital region, imbricate, strongly keeled. Body slender, 59 rows of scales around midbody, of these 10–12 rows of scales on back, from occiput to pectoral region homogenous in size, shape, slightly larger than those on neck, imbricate, pointed, keeled, and directed posteriorly forming regularly arranged longitudinal rows; those on flanks heterogeneous in size, shape,

smaller than those on back, obtusely pointed, keeled, with irregularly scattered, slightly larger, pointed, keeled scales; scales of upper rows directed backwards and upwards; ventral rows backwards and downwards; ventral scales subimbricate, keeled, homogenous in size, shape, arranged in 65 rows; no precloacal or femoral pores. 48 scales in a row from nape to the cloaca. Fore and hind limbs relatively slender, tibia short (CL/SVL ratio 0.37); digits moderately long, ending in strong, elongate, slightly recurved claw; inter-digital webbing absent; subdigital lamellae entire, tri-mucronate, 22 subdigital lamellae on toe IV; relative length of fingers $4 > 3 > 2 > 5 > 1$, toes $4 > 3 > 2 > 1$. Fore and hind limbs covered above and below with regularly arranged, enlarged, pointed, strongly keeled scales. Enlarged projecting scale on thigh present. Tail entire; tail base swollen; tail uniformly covered



Fig. 3. *Sitana dharwarensis* sp. nov., holotype, ♂ (NCBS-AL142) in life.



Fig. 4. *Sitana dharwarensis* sp. nov., holotype, ♂ (NCBS-AL142) dewlap in life.

with similar sized, keeled, weakly pointed, regularly arranged, posteriorly directed imbricate scales, no enlarged subcaudal row.

Coloration in preservative (Fig. 1). Coloration much more faded, overall background coloration more yellowish. Rhomboidal marks turn much paler and are almost diffused towards the flank. Blue coloration on the lower chin turns black.

Coloration in life (Figs 3–4). Dark-brown above with five dark rhomboidal markings on the trunk, first mark present just posterior to the neck and the last one on the flank. Each rhomboidal blotch has a light colored line running through it along the vertebral column. Limbs brown, banded with alternating dark and light bands. Head coloration same as the body, labials banded with light and dark bands. Dewlap yellowish white throughout with a steel-grey to blue line running from mental to a few scales below it. The colored line does not enter the dewlap and terminates just before the enlarged dewlap scales. Ventrally white.

Etymology. The specific epithet refers to the Dharwar Craton where the species is distributed.

Variation. The paratypes resemble the holotype in most aspects except for ventral belly scale number. The paratype male possesses 31–32 scales. Other morphometric and meristic characteristics are presented in Table 1.

Natural history. A species inhabiting open dry scrub and rock terrain in northern Karnataka. The type locality is a barren hillock adjacent to a seasonal river. The locality is heavily disturbed from activities relating to stone quarrying. The species is common at the type locality and is found in gardens in the town. Other sympatric reptiles observed are *Eutropis* cf. *carinata*, *Hemidactylus parvimaculatus* Deraniyagala, 1953 and *Hemidactylus*

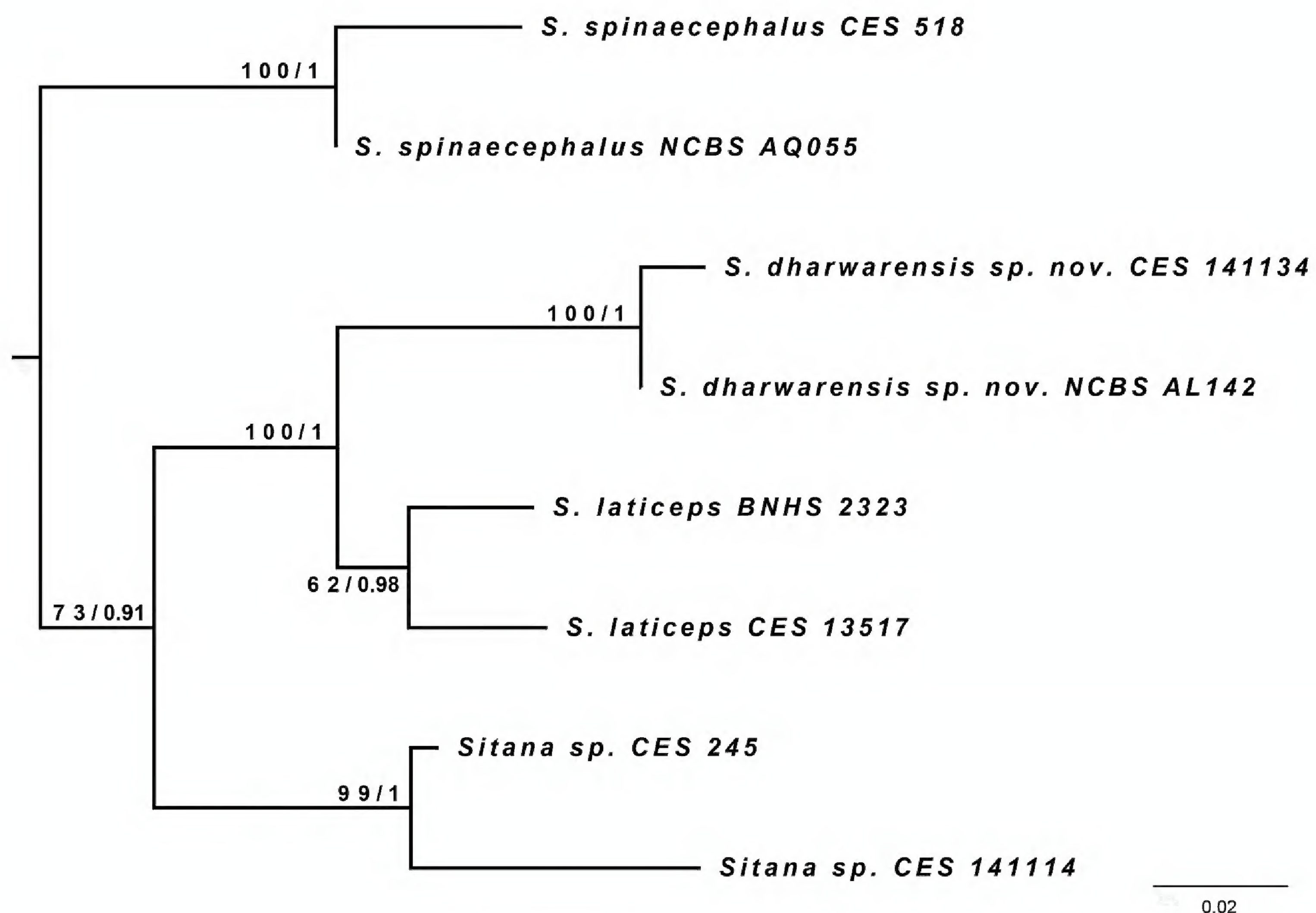


Fig. 5. Maximum Likelihood phylogeny based on 1011bp of ND2 and 649np of R35 gene for selected *Sitana* species. Numbers at nodes indicate ML/BI support.

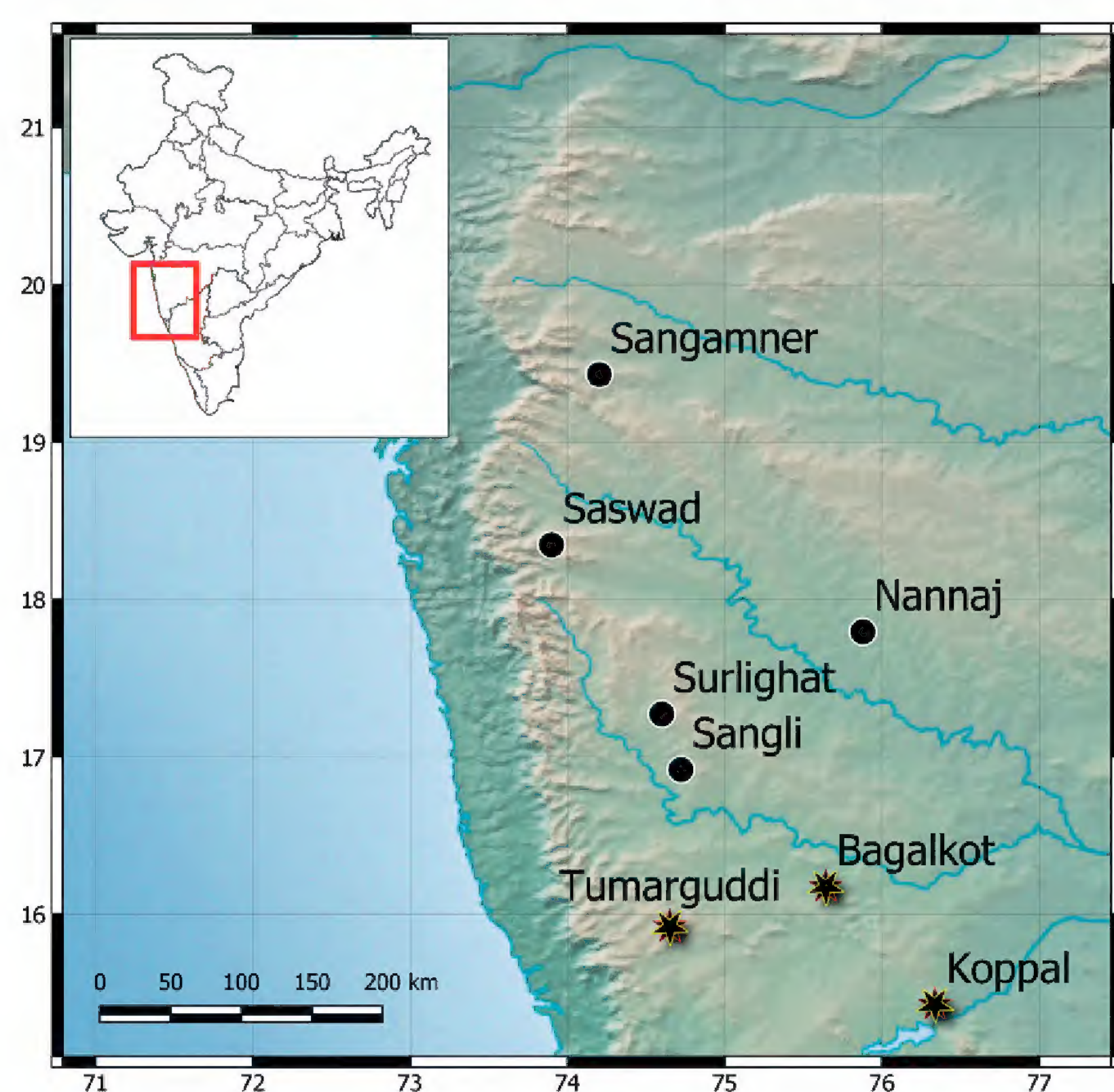


Fig. 6. Map of south western India showing distribution of *Sitana laticeps* (black circle) and *S. dharwarensis* sp. nov. (asterisk). Inset map shows main map highlighted by the red square.

vijayraghavani Mirza, 2018. Based on available mtDNA ND2 gene sequences, the species appears to be distrib-

uted south of a tributary (Panchgana) of Krishna River at the following localities: Bagalkot, Tumarguddi and Koppal.

DISCUSSION

Molecular phylogenetics based on a fragment of mitochondrial ND2 and nuclear R35 gene recovered *Sitana dharwarensis* sp. nov. embedded within a clade containing *S. laticeps* and *S. spinaecephalus* and was recovered as sister taxon to *S. laticeps* with high support from ML (bootstrap 100) & BI (posterior probability 1.0) (Fig. 5). The new species is 3–4% (un-corrected p-distance for ND2 gene) divergent from available sequences of *S. laticeps*. Additionally, the new species is distributed south of Panchganga River, a tributary of Krishna River, whereas *S. laticeps* is distributed north of the river (Fig. 6). The new species appears to be restricted to the area encompassed by the two major rivers Krishna and Tungabhadra. A parallel case appears to be that of the newly described *Hemidactylus vijayraghavani* (Mirza, 2018) from the same locality. These rivers likely act as biogeographic barriers for terrestrial lizards as seen in species of the genus *Sitana* (Deepak et al. 2016; Deepak & Karanth 2017). The sequences of specimens CES 245 and CES

141114 used in the phylogenetic analysis potentially represent a new species.

Description of yet another species of the genus *Sitana* is not surprising as recent studies provided hints on the presence of immense genetic diversity across sampled populations (Deepak & Karanth 2017). With additional sampling, the number of *Sitana* species in the subcontinent will certainly rise. Morphologically cryptic species currently considered conspecific with broadly distributed species, a common case with most lizard species recorded from India (Agarwal et al. 2014; Agarwal & Ramakrishnan 2017; Deepak & Karanth 2017; Mirza et al. 2018), represent a major subset of the reptilian diversity of the country and hence dedicated efforts must be made to document and describe these. Many of these newly described species occur outside of protected areas and in most localities, local populations are at risk from being wiped out. A management plan for non-protected area, especially open and scrublands that are otherwise termed wasteland and considered less biodiverse must be devised to ensure protection of species and habitats.

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The scale insect (Hemiptera: Coccoomorpha) collection of the entomological museum “Universidad Nacional Agronomía Bogotá”, and its impact on Colombian coccidology

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Abstract. Acquisition of local and global biodiversity knowledge demands immediate and long-term efforts, both tutoring new generations of taxonomists and establishing, maintaining and improving research collections. Through biodiversity studies, the entomological museum “Universidad Nacional Agronomía Bogotá” (Bogotá, Colombia) has been developed and has built up a substantial collection of scale insects (Hemiptera: Coccoomorpha), with 7,052 slide-mounted specimens and close to 800 alcohol-preserved samples representing 115 species belonging to 59 genera and nine families. This insect group is exclusively phytophagous, and many species are pests on economically important crops in Colombia. Curation of scale insect specimens includes slide mounting, identification, cataloging and databasing. Ecological and geospatial analyses of field data have identified insect-host interactions, and areas of the country where new field collections should be made. Host-insect interaction analysis has shown that coffee is the host-plant with the largest number of associated scales, *Rhizoecus cacticans* (Hambleton, 1946) and *Rh. colombiensis* Ramos & Caballero, 2016 are the scale species with the largest host-plant range; and *Geococcus coffeae* Green, 1933 and *Puto barberi* (Cockerell, 1895) are the commonest scale species. Altitudinal and geographic distribution analysis have shown that sampling efforts have been concentrated in the central region, while the northern and southeastern regions of Colombia have been poorly collected. These analyses provide a guideline for future studies, such as which zones should be sampled and which host-plant species have information gaps in their documented distributions and scale insect-host interactions. The museum’s large number of specimens, species diversity representation and rich associated biological data indicate that the scale insect collection of the “Universidad Nacional Agronomía Bogotá” entomological museum is the most important in Colombia.

Key words. Alpha taxonomy, biodiversity conservation, Neotropical, South America, Sternorrhyncha.

INTRODUCTION

The scale insects (Hemiptera: Sternorrhyncha: Coccoomorpha) are comprised of 55 families (20 of them extinct) and more than 8,000 extant species worldwide (García Morales et al. 2016). In Colombia, 252 species have been recorded, representing 13 families, with hosts in more than 40 plant families. The scale insect families with the greatest diversity are Diaspididae (with 32% of recorded species), followed by Pseudococcidae (26%),

Coccidae (17%) and Rhizoecidae (10%) (García Morales et al. 2016).

The Coccoomorpha is an important group due to its economic impact on agriculture worldwide (Kondo 2001; Gullan & Martin 2003). In Colombia, over 100 species have been recorded attacking crops such as avocado (*Persea americana* Mill., 1768), banana (*Musa paradisiaca* L., 1753), cacao (*Theobroma cacao* L., 1753), coffee (*Coffea arabica* L., 1753), sugarcane (*Saccharum officinarum* L., 1753), citrus (*Citrus* sp.), oil palm (*Elaeis guineensis* Jacq., 1763), mango (*Mangifera indica* L.,

1753) and cassava (*Manihot esculenta* Crantz, 1766) (Figuerola 1977; Castillo & Bellotti 1990; Gallego & Vélez 1992; Kondo 2001; Kondo et al. 2008; Caballero et al. 2017, 2019; Ramos-Portilla & Caballero 2017). At the international level, several scale insect species are considered to be quarantine pest risks by the Colombian phytosanitary protection organization, Instituto Colombiano Agropecuario (ICA). Its Resolution 3593 (Instituto Colombiano Agropecuario 2015) includes scale insects such as *Aonidiella aurantii* (Maskell, 1879), *Comstockaspis perniciosus* (Comstock, 1881) and *Aulacaspis rosae* (Bouché, 1833) (Diaspididae), *Eulecanium tiliae* (L., 1758) (Coccidae), *Icerya aegyptiaca* (Douglas, 1890) and *I. seychellarum* (Westwood, 1855) (Monophlebidae), and *Maconellicoccus hirsutus* (Green, 1908) and *Pseudococcus calceolariae* (Maskell, 1879) (Pseudococcidae). As endemic quarantine pest risks, the following scale insects were mentioned: *Coccus hesperidum* L., 1758, *Saissetia coffeae* (Walker, 1852), *Icerya purchasi* Maskell, 1879 and *Selenaspidus articulatus* (Morgan, 1889) (Instituto Colombiano Agropecuario 2015).

The chronology of coccidology in Colombia

The first scale insect species described from Colombia was *Coccus caudatus* by F. Walker in 1852, based on a male specimen. It came from a personal collection without information on its host or locality and is conserved in the British Museum (Natural History) in London, U.K. (Walker 1852). Cocomorpha studies in Colombia began in 1929, when F. Laing described *Crenulaspidiotus murellae* and *Acanthococcus tucurinae* from samples collected in Magdalena department (Laing 1929). The entomologist L. Murillo was the first Colombian to describe a scale insect species, *Puto antioquiensis* from samples taken on roots of *Coffea arabica* in the department of Antioquia (Murillo 1931). Over the next two decades, 23 new species from various departments of Colombia were described by F. Laing, E. Hambleton, N. S. Borchsenius, R. Mamet and A. S. Balachowsky (Laing 1929; Hambleton 1946; Mamet 1954; Balachowsky 1957, 1959a, b; Beardsley 1986; Williams & Granara de Willink 1992; Gimpel & Miller 1996;).

The Russian-born French entomologist A. S. Balachowsky was one of the most important contributors to the coccidology of Colombia. He published descriptions of 16 species of Diaspididae, Eriococcidae, Pseudococcidae and Rhizoecidae. He also provided information from samples he collected when visiting Colombia in the 1950s and his slide-mounted specimens are conserved in the Muséum National d'Histoire Naturelle in France (Balachowsky 1957, 1959a, b). The first Colombian entomologist to conduct pioneering scale insect inventories for the country was A. Figuerola: he listed five families, 34 genera and 53 species, including new records and lists of host plants (Figuerola 1946, 1952, 1977). So far, there

is no information regarding the whereabouts of his collection (Caballero et al. 2017). Figuerola was followed by F. Mosquera, who published two important papers about the genus *Ceroplastes* (Coccidae) in Colombia, in which he listed seven species, six of them presented as new (Mosquera 1979, 1984). Slide-mounted specimens representing those species are currently preserved in the Colección Taxonómica Nacional de Insectos “Luis Maria Murillo” (Colombia).

The last part of the 20th century was characterized by important efforts on the recognition of species in Colombia, carried out by several national and international researchers. Castillo & Bellotti (1990) listed mealybugs (Pseudococcidae) associated with cassava, from which slide-mounted specimens are preserved in the International Center of Tropical Agricultural (CIAT) collection. Likewise, Gallego & Vélez (1992) increased the number of families, genera and species of Coccoidea recorded, particularly for the families Diaspididae, Pseudococcidae and Coccidae. In the same year, Williams & Granara de Willink (1992) listed and described eight species of mealybugs (Pseudococcidae, Putoidae and Rhizoecidae) from Colombia. Posada (1989), in his treatise on insects in agriculture, updated the species list of Coccoidea for Colombia to 114 taxa (93 of them to species level), associated with more than 60 economically important crops.

In the 21st century, Colombian coccidology has been characterized by a new insight. Through reviewing previous contributions, the coccidologist Dr. Takumasa Kondo has led the investigation in Colombia and in the world, publishing more than 120 peer-reviewed papers. He has been working constantly to update the list of scale insects in the country, and has described more than 50 new species, 14 of them from specimens collected in Colombia: *Akermes colombiensis* Kondo & Williams, 2004, *Austrotachardiella colombiana* Kondo & Gullan, 2005, *Leptococcus rodmani* Kondo, 2008, *Neotoumeyella caliensis* Kondo & Williams, 2009, *Crypticerya multicicatrices* Kondo & Unruh, 2009, *Bombacoccus aguacatae* Kondo, 2010, *Cryptostigma philwardi* Kondo, 2010, *Foldilecanium multisetosum* Kondo, 2011, *Hemilecanium guanabana* Kondo & Hodgson, 2013, *Toumeyella coffeae* Kondo, 2013, *Pulvinaria caballeroramosae* Tanaka & Kondo, 2015, *Capulinia linarosae* Kondo & Gullan, 2016, *Cryptinglisia corpoica* Kondo & Montes, 2018, *Cryptinglisia ica* Montes & Kondo, 2018 (Kondo & Williams 2004, 2009; Kondo & Gullan 2005, 2008; Kondo & Unruh 2009; Kondo 2010a, b, 2011, 2013; Kondo & Hodgson 2013; Tanaka & Kondo 2015; Kondo et al. 2016a, 2018).

The Entomological Museum UNAB and its scale insect collection

The northernmost region of South America, the so-called Tropical Andes Hotspot, is considered to be the most

biodiverse region on Earth (Conservation International 2005), and this richly biodiverse realm is under persistent threat from human activities such as mining, timber extraction, oil exploration, extensive monocrop cultivation, and illegal trafficking of fauna and flora (FAO 2019). In order to preserve and study that biodiversity, specialized insect collections in universities play an essential role in training new generations of entomologists. In 2001, the Faculty of Agronomy (FA) at the Universidad Nacional de Colombia, Bogotá, designated the “Universidad Nacional Agronomía Bogotá” (UNAB) museum as a “*Scientific Center for research and student learning of Insect Systematics*” related to agriculture (Sistema de Patrimonio Cultural y Museos 2008). One of the greatest achievements at the UNAB museum is the collection and curation of close to 180,000 dry-mounted specimens, 18,400 larvae and adults preserved in alcohol, and 10,430 slide-mounted specimens as follows (rounded numbers): Coccothorax (7000 slides), Collembola (1700), Aphidomorpha (1400), Aleyrodomorpha (500), Thysanoptera (90), Acari (90) and Psyllomorpha (50 slides). Overall, the museum’s collections represent 4,000 species, 150 families, and 19 insect orders (Serna et al. 2017).

In the last five years there has been a notable effort to build the Scale Insect Collection at UNAB (hereafter referred SIC-UNAB) to become the most important collection of this insect group in the country and one of the most important in South America. This development is derived from undergraduate and graduate theses and studies and has contributed to the knowledge of Colombian scale insect biodiversity with descriptions of new species and new collection records. Moreover, the SIC-UNAB has received contributions by recognized coccidologists like Douglass Miller (USDA Animal and Plant Health Inspection Service, U.S.A.), Penelope Gullan (Australian National University, Australia), Takumasa Kondo (Corporación Colombiana de Investigación Agropecuaria, Colombia), Lucía Claps and Patricia Gonzalez (Universidad Nacional de Tucumán, Argentina), Bora Kaydan (Çukurova University, Turkey) and Ana Lucia Peronti (São Paulo State University, Brazil).

In view of the economic impact of scale insects and the lack of knowledge about their diversity in Colombia, our aim is to present the status of the SIC-UNAB and acquaint the coccidologist community with the most important scale insect collection in Colombia and one of the most important in South America. Furthermore, our intention is to encourage coccidologists to consider the SIC-UNAB as a partner to develop new taxonomic studies and specimen exchanges.

MATERIALS AND METHODS

The specimens deposited in the SIC-UNAB are composed mainly of insect samples collected by students and specialists from the Universidad Nacional de Colombia. The two most significant sources of samples are from (1) Dr. Andrea Ramos working in partnership with Instituto Colombiano Agropecuario (ICA), and (2) the sampling conducted by the Centro de Investigación del Café (Cenicafé). The first covered 12 departments of Colombia focused on the main economically important crops (i.e., *Musa* sp., *Theobroma cacao*, *Coffea* sp., *Citrus* sp. and *Saccharum officinarum*). The second was carried out in seven departments and aimed to record the scale insects associated with coffee roots. Other sources of samples include the Corporación Colombiana de Investigación Agropecuaria (Agrosavia), the Banana Association of Colombia (AUGURA), Bogotá Botanical Garden “Jose Celestino Mutis”, and exchanges with national and international entomological museums.

The first scale insect slides were made using different protocols, such as those standardized by Williams & Granara de Willink (1992) and the Systematic Entomology Laboratory (2015), U.S. Department of Agriculture, Beltsville, MD, U.S.A. Since 2016, SIC-UNAB has switched to a modification of the method established by Sirisena et al. (2013), as the process is faster and avoids the use of some carcinogenic compounds (xylene and phenol). All samples are preserved as permanent slide-mounts in Canada balsam.



Fig. 1. A. Slide holder with samples curated. B. Slide of a curated sample, showing the arrangement of collection and identification data labels and specimen.

Identifications and imaging have been carried out using a Nikon Eclipse E600 and Zeiss Axio Lab.A1 phase contrast compound microscopes, a Lumenera Infinity 1-5C and AxioCam ERc 5s microscope cameras, and the photograph editing software Image-Pro Insight version 8.0. Taxonomic determinations are supported by publications, comparisons with voucher specimens and specialist corroborations. The data systematization is made using Microsoft Excel 2017® software.

Curatorship is based on the protocol given by Martínez-Alava & Serna (2015). The scale insect database is composed of field data and taxonomic information, i.e., genus, family, order, identifier, identifier institution, identification date (dd-mmm-yyyy), curator observations, number of specimens, sex, development stage of specimens, and voucher specimens conserved in ethanol. The liquid voucher specimens are preserved in 75% ethanol with the same labels inside the vials (Fig. 1).

A simple scale insect-host interaction network analysis was performed with the information available in the collection. The matrix used for the analyses comprised quantitative data of the number of associations recorded in the SIC-UNAB database between scale insect species (rows) and plant hosts (columns). Network metrics were calculated as follows: i) number of nodes or total number of species of the network as the sum of the number of scale insect species with host record and the number of host-plant species, ii) linkage density as total number of interactions divided by the total number of plant and insects species in the network, iii) connectance as the proportion of actually observed interactions to all possible interactions, being 0 when there are no interactions and 1 when all species interact, and iv) H_2 as the network-level specialization measure, based on the deviation of the number of interactions of a species and the expected number of interactions of each species (Blüthgen et al. 2006; Dormann et al. 2009; Delmas et al. 2019). Also, bipartite graphs representing the linkage between species were constructed. Interaction analysis and figures were performed with a *bipartite* package (Dormann et al. 2008) in the open-license software R version 3.5.2 (R Development Core Team 2019).

Available data about altitude (m a.s.l.) and location (decimal degree coordinates) were used to plot the pattern of altitudinal and geographical distribution. The altimetry graphic was built in the console RWizard (Guisan et al. 2014), based on the free statistical software R version 3.5.2 (R Development Core Team 2019). The geographic distribution map was developed with the software DIVA-GIS version 7.5.0, with a physical map layer designed by Milenioscuro, CC BY-SA 3.0 (Milenioscuro 2009).

RESULTS AND DISCUSSION

To date, the SIC-UNAB preserves 7,052 curated specimens, resulting from more than 1,000 samples. The collection has records of 131 taxa, of which 115 are identified to species level, 3 are identified as species complexes and 13 identified to genus level (see Appendix I: Table 1). The 115 species belong to 57 genera and nine families. The highest diversity is represented by species of Pseudococcidae (34.1%), followed by Rhizoecidae (23.2%). The remainder of the species are divided between Diaspididae (18.8%), Coccidae (10.9%), Ortheziidae (2.9%), Monophlebidae (2.9%), Asterolecaniidae (2.2%), Putoidae (2.2%), Eriococcidae (1.4%), Dactylopiidae (0.7%) and Margarodidae (0.7%). Worldwide, the most diverse scale insects families are Diaspididae (> 2,600 spp.), Pseudococcidae (> 2,000 spp.) and Coccidae (> 1,100 spp.), but SIC-UNAB conserves a rich representation of Pseudococcidae and Rhizoecidae because the research projects that have provided samples to the collection were focused on the diversity of mealybugs in the broad sense, i.e., Pseudococcidae, Rhizoecidae and Putoidae.

The scale insects-host interaction network based on samples deposited in the SIC-UNAB is shown in Figure 2. The interaction network based on the information available at the SIC-UNAB consisted of 222 nodes, corresponding to a total of the scale insect species and their host-plant species. Of the 131 taxa, 120 have host data, with 102 plant species. In the network, 227 interactions or links were recorded, with a density of 1.023 links per species. Around 70% of the scale insect species are recorded with only one host-plant species.

The network metrics of the data were low, with a connectance value of 0.019 and H_2 of 0.604. Connectance values close to zero indicate little interaction between the species, and the low H_2 index indicates a high level of specialization of the species in the network. These metrics provide preliminary knowledge of the association between scale insects and their hosts in Colombia.

The scale insect species with the highest number of interaction records (grade) with host plants are *Rhizoecus cacticans* (Hambleton, 1946) and *Rhizoecus colombiensis* Ramos & Caballero, 2016. The polyphagous habit of *R. cacticans* is confirmed and its range of host records is increased. The SIC-UNAB conserves samples of this species associated with 34 hosts, of which 23 are new records (Appendix I: Table 1). This new information broadens its host-range from 32 to 53 plant species. *Rhizoecus colombiensis* was described from specimens collected and preserved in SIC-UNAB, hence most of the hosts that have been recorded for this species are the same as are presented in this paper, except for four plant species recorded here for the first time (see underlined names of hosts in Appendix I: Table 1).

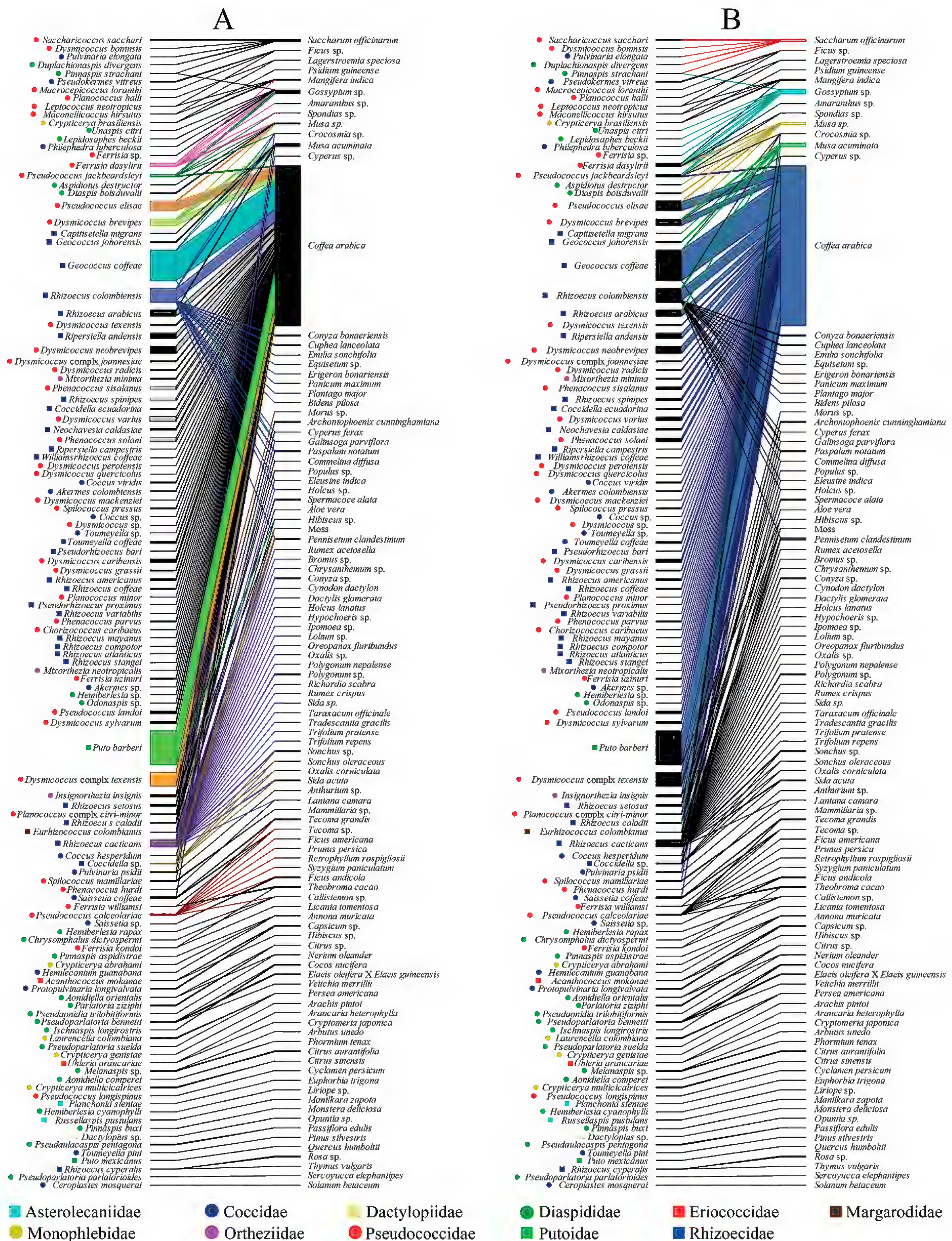


Fig. 2. Interaction network of association between scale insects and hosts based on storage samples in the scale insect collection of the entomological museum “Universidad Nacional Agronomía Bogotá” (SIC–UNAB). **A.** The bipartite graph on the left emphasizes scale insect species with the same color indicating the rectangle of the species and the line of the link. **B.** The graph on the right emphasizes plant hosts and their links. The width of the rectangle next to each species name is proportional to the sum of interactions involving this species, while the width of the lines linking scale insect species and plant species is again proportional to the number of interactions between the connected species.

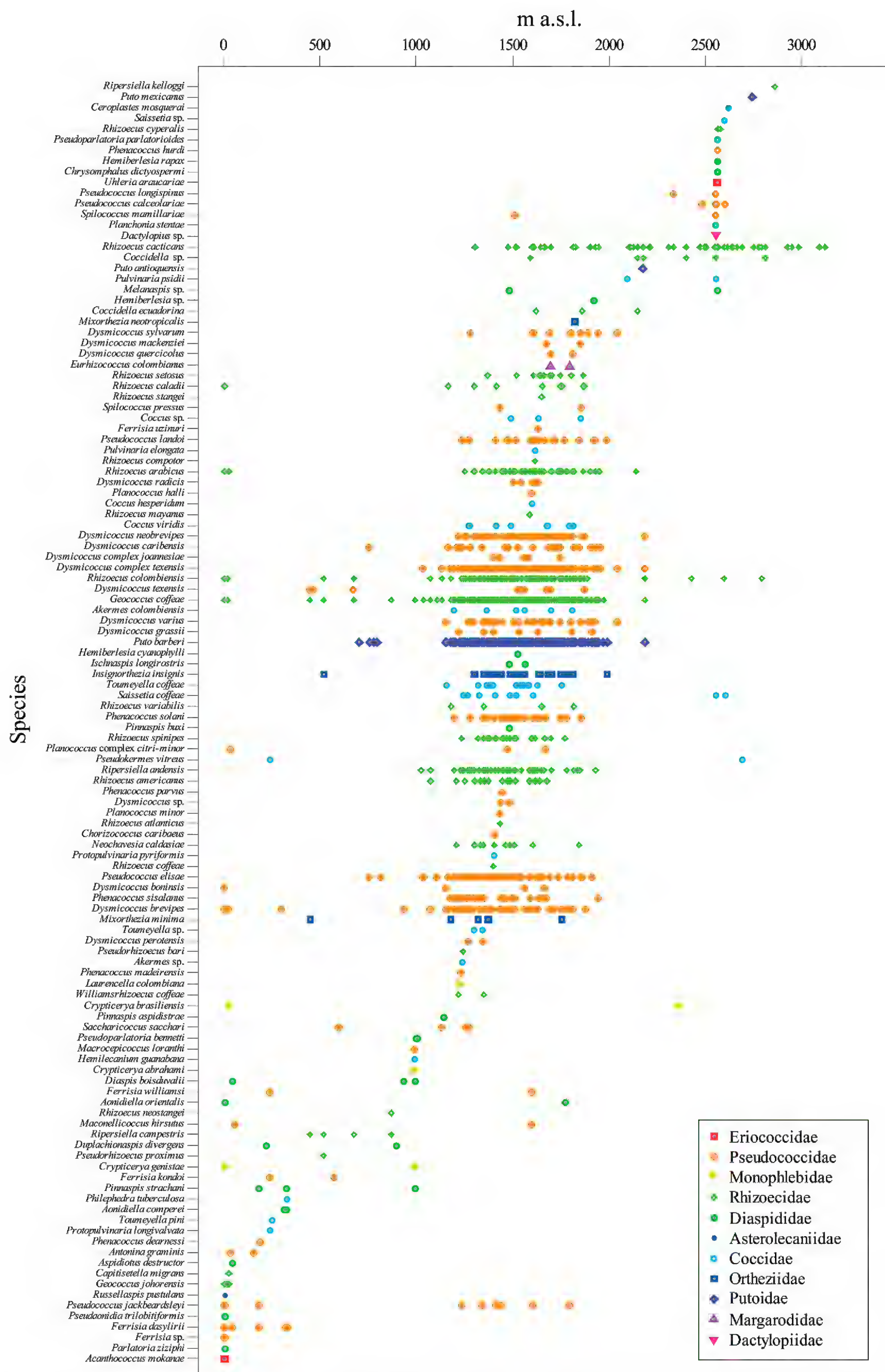


Fig. 3. Altimetry graphic with range by species given in meters about sea level (m a.s.l.). Each point indicates one sample. Color and shape indicate taxonomic family.

Puto barberi (Cockerell, 1895) and *Geococcus coffeae* (Green, 1933) are the species most recurrent in the collection samples (Fig. 2 A), but this contrasts with their host associations. Both species have several samples on *Coffea arabica* (Rubiaceae), due to the large sampling effort on coffee in one of the most important projects that built the collection (Caballero et al. 2018, 2019). *Puto barberi* is recorded in association with *Hibiscus* sp. (Malvaceae), however, this species is polyphagous and has been recorded from more than 50 plant species (Williams et al. 2011; García Morales et al. 2016). *Geococcus coffeae* is also polyphagous, associated with 63 plant species (Williams 1968; García Morales et al. 2016), however, in the collection it is recorded on only four hosts, one of them corresponding to an earlier record (*C. arabica*) and three new records, i.e., *Crocasmia* sp. (Iridiaceae), *Galinsoga parviflora* (Asteraceae) and *Musa acuminata* (Musaceae).

The plant species with the highest number of interactions with scale insect species (63) was *C. arabica*, which is also an indicator of the large sampling effort in coffee cultivation. The remaining plant species are recorded in association with no more than seven species of scale insects (Fig. 2B).

The focus of the UNAB museum is agricultural entomological diversity, which means the study of arthropods associated with plant species of agricultural importance. As a result of different studies, the SIC-UNAB preserves samples that represent 45% (63 species) of the worldwide scale insect diversity recorded on *C. arabica*, which is 141 species (García Morales et al. 2016; Caballero et al. 2019). Other plants of agricultural importance for Colombia are cotton (*Gossypium* sp.) and plantain (*Musa acuminata* Colla, 1820), both with seven scale insect species recorded, banana (*Musa paradisiaca*) with six; sugarcane (*Saccharum officinarum*) with five; mango (*Mangifera indica*) with four; and soursop (*Annona muricata* L., 1753) with three. The number of associations are indicated in Figure 2B.

Altitudinal and geographic distribution

The analysis showed that *Rhizoecus colombiensis* is the species with the widest altitude range, being present from 6 m a.s.l. on *M. acuminata* to 2,792 m a.s.l. on *Holcus* sp. (Poaceae) (Fig. 3). The species is polyphagous (Ramos-Portilla & Caballero 2016) and its hosts include banana and plantains (*Musa* sp.), which can grow from sea level up 2,000 m a.s.l., *Coffea arabica*, which can grow between 1,000 and 2,300 m a.s.l. (Federación Nacional de Cafeteros 2013), and *Holcus* sp. which is able to grow up to 3,300 m a.s.l. (Apráez et al. 2019). Other species with wider altitude range are *R. arabicus*, *R. cacticans* and *G. coffeae* (Rhizoecidae) which cover around 2,000 meter. *Rhizoecus arabicus* and *G. coffeae*

were found from sea level to 2,200 m a.s.l., and *R. cacticans* from 1,200 m a.s.l. to 3,100 m a.s.l.

Pseudokermes vitreus (Cockerell, 1894) and *Crypticerya brasiliensis* (Hempel, 1900) both present a special situation. For each of these species there are only two samples, and in each case, the samples are from extreme altitude points with more to 2,000 meters between them (Fig. 3). The altitude points for *P. vitreus* are 244 and 2,694 m a.s.l. in Caquetá and Boyacá departments, respectively. *Crypticerya brasiliensis* was found at 24 and 2,357 m a.s.l., in Providencia Island and Boyacá, respectively. These data agree with previously recorded information on both species, which are polyphagous and associated with plants from warm and temperate regions (Kondo & Hardy 2008; García Morales et al. 2016; Kondo et al. 2016b).

Regarding the geographic distribution, the SIC-UNAB has an important representation of the Colombian Cocomorpha fauna from the Andean and Caribbean biogeographic regions (Fig. 4). This bias is due to UNAB projects that have been focused on coffee crops, which are mostly cultivated in the Andean region.

A sanctuary for scale insects in Colombia

Research on SIC-UNAB has provided new records of species and hosts for Colombia and Mexico, taxonomic keys and descriptions of new scale insect species found on crops such as citrus, sugarcane and coffee (Kondo et al. 2016b; Ramos-Portilla & Caballero 2016, 2017; Caballero et al. 2017, 2018; Caballero & Ramos-Portilla 2018). In addition, the collection has authoritative taxonomic determinations and stores type material of *Acanthococcus mokanae* González, Ramos & Caballero, 2019, *Ferrisia williamsi* Kaydan & Gullan, 2012, *Rhizoecus colombiensis* Ramos & Caballero, 2016, *Pseudorhizoecus bari* Caballero & Ramos, 2018, *Tillancoccus koreguajae* Caballero & Ramos, 2018 and *Williamsrhizoecus coffeae* Caballero & Ramos, 2018 (see Appendix I: Table 1).

Compared to the main scale insect collections of Colombia, the SIC-UNAB conserves the most significant collection, as we show below:

Instituto Alexander Von Humbolt (IAVH): No scale insect specimens (J.C. Neita, Bogotá, pers. comm. 2020).

International Center for Tropical Agriculture Arthropod Reference Collection (CIATARC): 259 slide-mounted scale insect specimens, 84 voucher liquid samples, representing six families, 21 genera, and 29 species (data of genera and species no provided) (M.I. Gómez, Valle del Cauca, pers. Comm. 2019).

Colección Taxonómica Nacional de Insectos Luis Maria Murillo (CTNI): 631 slide-mounted specimens of two families: Coccidae with six genera and 14 species, Rhizoecidae one genus and one species. This collection conserves type material of *Bombacoccus aguacatae* Kondo, 2010 (holotype), *Ceroplastes boyacensis* Mosquera, 1979

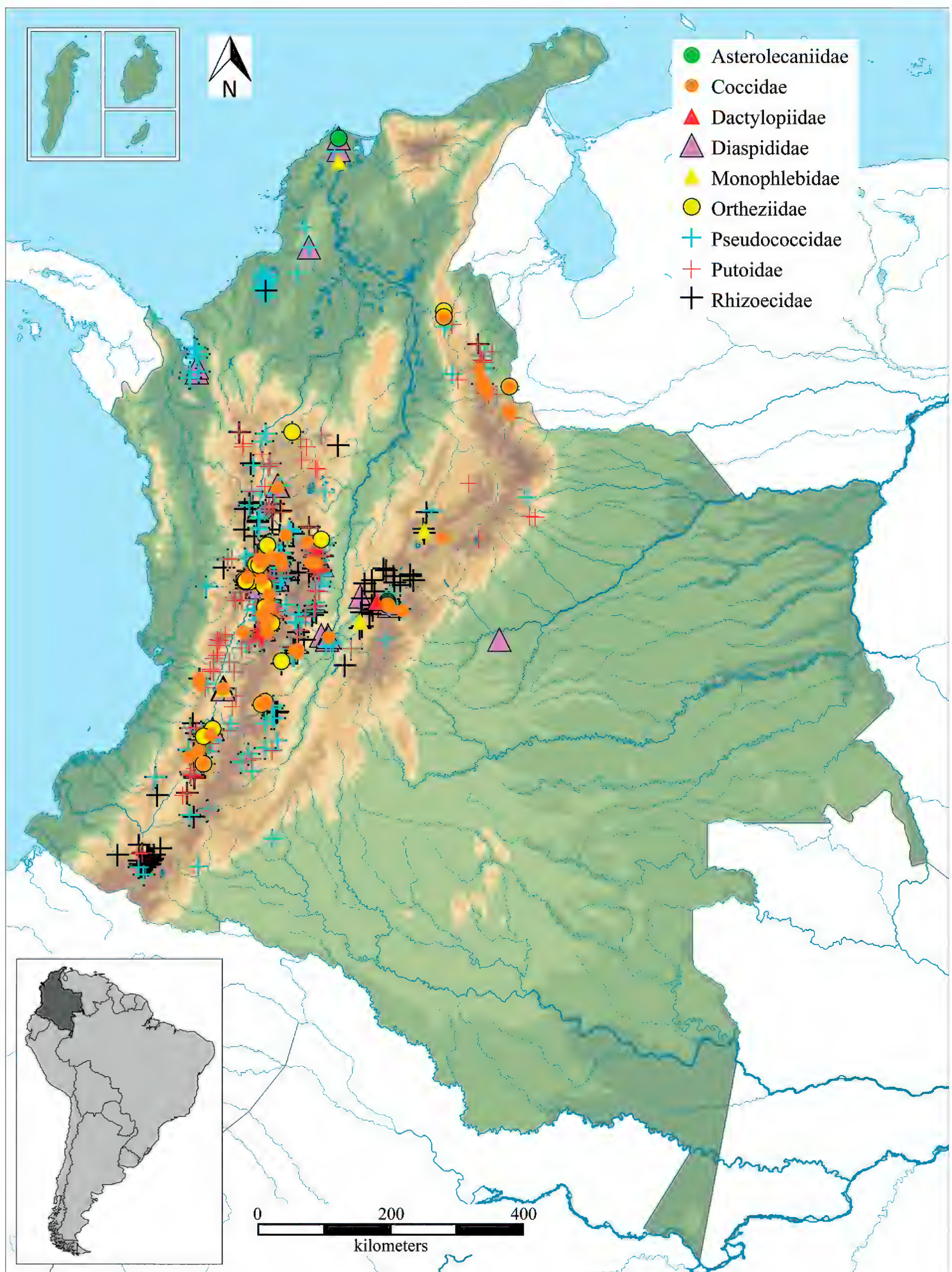


Fig. 4. Map of Colombia with distribution of Coccoomorpha samples under conservation in Scale Insect Collection of entomological museum "Universidad Nacional Agronomía Bogotá" (SIC-UNAB). Samples discriminated by families with symbols and colors.

(holotype and paratypes), *Ceroplastes cundinamaricensis* Mosquera, 1979 (holotype and paratypes), *Ceroplastes martinae* Mosquera, 1979 (holotype and paratypes), *Ceroplastes mosquerasi* Ben-Dov, 1993 (holotype and paratypes), *Ceroplastes ocreus* Mosquera, 1984 (holotype and paratypes), *Ceroplastes trochezi* Mosquera, 1979 (holotype and paratypes), *Cryptinglisia corpoica* Kondo & Montes (holotype and paratypes), *Cryptinglisia ica* Montes & Kondo (holotype and paratypes), *Pulvinaria caballeroramosae* Tanaka & Kondo, 2015 (paratypes), and *Rhizoecus colombiensis* Ramos-Portilla & Caballero, 2016 (paratype) (E. Vergara, Bogotá, pers. Comm. 2020)

Museo Entomológico Francisco Luis Gallego (ME-FLG): 52 slide-mounted scale insect specimens. Pseudococcidae: 13 genera, 24 species. Diaspididae: 15 genera, 22 species. Margarodidae: seven genera, eight species. Coccidae: 13 genera, 19 species. (J. Quiroz, Medellín, pers. Comm. 2019)

Museo de Historia Natural del Instituto de Ciencias Naturales (ICN): 15 slide-mounted scale insect specimen of families Pseudococcidae and Coccidae (data of genera and species no provided). This collection conserves material Type of *Leptococcus rodmani* Kondo, 2008 (paratype) and *Akermes colombiensis* Kondo & Williams, 2004 (paratype). (F. Fernandez, Bogotá, pers. Comm. 2019)

Universidad Nacional Agronomía Bogotá (UNAB): 7,052 slides-mounted scale insects specimens (details in Appendix I: Table 1).

New records for Colombia

***Geococcus johorensis* Williams, 1969** [UNAB N° cat. 1861]* COLOMBIA: Antioquia, Apartadó, Vda. Churidó, Fca. Villa Nancy, 7°47'38.72" N, 76°38'56.94" W, 27 m a.s.l., ex roots *Musa acuminata* (AAB) (Musaceae), Feb-2015, collector N. Herrera, 6 ♀♀ adults; Antioquia, Carepa, Vda. Las Trecientas, Fca. Villa Adis, 7°46'56.93" N, 76°46'6.56" W, 17 m a.s.l., ex roots *Musa acuminata* (AAB) (Musaceae), Feb-2015, collector O. Giraldo, 7 ♀♀ adults; Antioquia, Chigorodó, Vda. Saden Guacamaya, Fca. Las Anitas, 7°42'45.86" N, 76°46'23.09" W, 6 m a.s.l., ex roots *Musa acuminata* (AAB) (Musaceae), Feb-2015, collector N. Herrera, 3 ♀♀ adults; Antioquia, Chigorodó, Vda. Saden Candelaria, Fca. Doña Mayo, 7°42'50.26" N, 76°46'6.56" W, 6 m a.s.l., ex roots *Musa acuminata* (AAB) (Musaceae), Feb-2015, collector O. Giraldo, 6 ♀♀ adults; Antioquia, Chigorodó, Vda. Saden Colorada, Fca. San Ignacio, 7°42'18.72" N, 76°46'23.09" W, 6 m a.s.l., ex *Musa acuminata* (AAB) (Musaceae), Feb-2015, collector L. Escobar, 5 ♀♀ adults; Antioquia, Turbo, Vda. Barro Colorado, Fca. Villa Arelis, 8°1'43.18" N, 76°39'26.89" W, 26 m a.s.l., ex roots *Musa acuminata* (AAB) (Musaceae), Feb-2015, collector N. Herrera, 4 ♀♀ adults; Antioquia, Turbo, Vda. Barro Colorado, Fca. La Mejor Es-

quina N° 2, 8°1'55.45" N, 76°39'56.52" W, 25 m a.s.l., ex roots *Musa acuminata* (AAB) (Musaceae), Feb-2015, collector O. Giraldo, 2 ♀♀ adults; Antioquia, Turbo, Vda. La Esperanza, Fca. La Esperanza, 8°5'43.76" N, 76°40'16.68" W, 21 m a.s.l., ex roots *Musa acuminata* (AAB) (Musaceae), Feb-2015, collector L. Escobar, 2 ♀♀ adults; Antioquia, Turbo, Vda. Villa María, Fca. Los Tres Hermanos, 8°6'41.98" N, 76°42'24.52" W, 5 m. a.s.l. ex roots *Musa acuminata* (AAB) (Musaceae), Feb-2015, collector L. Escobar, 5 ♀♀ adults.

*All samples with the same catalogue number.

***Phenacoccus hurdi* McKenzie, 1964** [UNAB N° cat. 1861] COLOMBIA: Cundinamarca, Bogotá D.C., Localidad Teusaquillo, Universidad Nacional de Colombia., 4°38'9.49" N, 74°5'20.22" W, 2564 m a.s.l., ex leaves, stems, and flowers of *Lantana camara* (Verbenaceae). 2-Abr-2012, collector A. Caballero, 10 ♀♀ adults.

***Puto mexicanus* (Cockerell, 1893)** [UNAB N° cat. 5538] COLOMBIA, Boyacá, Arcabuco, 5°44'17.00" N, 74°24'52.00" W, 2742 m a.s.l., ex leaves of *Quercus humboldtii* (Fagaceae). 10-Abr-2019, collector P. Rodríguez, 3 ♀♀ adults and 4 ♀♀ 3rd instars.

CONCLUSIONS

In a megadiverse country like Colombia, research to increase awareness of diversity, with taxonomy as the main tool, should be a priority. The entomological museum UNAB contributes to this crucial task through curation and conservation of specimens as vouchers of species richness. Its collection of scale insects has become the most important in Colombia due to the number of specimens, diversity of species and associated information on their geographical distribution. The information stored in this collection has contributed to the knowledge of Coccothraupis taxonomy and Colombian phytosanitary status, providing a list of 115 species, new records of three scale insects and 61 host plants and distribution information. Of the 252 species recorded so far for Colombia, the SIC-UNAB has 115 species i.e., 41% of total of the current Colombian Coccothraupis diversity. This collection provides new information about associations of scale insects with host plants of economic importance to Colombia, their locations, and confirmation of previous records. This information will be useful to phytosanitary authorities and will enable research centers to plan regulation and investigation activities.

The ecological analysis allowed us to infer the sampling frequency by species, and to identify association networks between scale insects and their hosts, and geospatial distributions. The analysis presented here gives an insight into how to direct and structure new research. Based on the geographic analysis, the SIC-UNAB should

redirect its field collecting to northern, west, and south-eastern Colombia, which coincides with biodiversity hotspots such as the Caribbean, Pacific and Amazonas regions. New analyses of species richness and host associations should be directed towards economically important crops to evaluate their impact in ecosystems of the country. Good examples might be banana and avocado crops, whose cultivated areas are substantial in Colombia and their production systems influence other associated plant species. Regarding identification methodology, so far the UNAB museum had used a morphological approach but in the future, it should include molecular techniques and ecological analysis as new information sources, trying to get closer to integrative taxonomy.

The mission of the entomological museum UNAB, as part of a public institution and as an element of the most important university in Colombia, is to provide information about Colombian insect diversity and related issues. In that sense, we encourage the coccidology community to consider the SIC-UNAB as a collaborating institution in future studies and for housing samples.

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APPENDIX I:

Table 1. List of species represented in the Scale Insect Collection at the UNAB entomological museum “Universidad Nacional Agronomía Bogotá” (SIC-UNAB), with information on location, host, catalogue number, material type, number of mounted specimens and liquid vouchers.

SPECIES	LOCALITY	HOST	CAT	HTY	PTY	SPCM (♀♀ adults)	LV
Asterolecaniidae							
<i>Planchonia stentae</i> (Brain,1920)	Cun	<i>Euphorbia trigona</i> (Euphorbiaceae)	4949			27	X
<i>Russellaspis pustulans</i> (Cockerell, 1892)	Atl	<i>Manilkara zapota</i> (Sapotaceae)	4973			15	X
Coccidae							
<i>Akermes colombiensis</i> Kondo & Williams, 2004	Ant, Cal, Cau, Qui	<i>Coffea arabica</i> (Rubiaceae)	3494			41	X
<i>Akermes</i> sp.	Qui	<i>Coffea arabica</i> (Rubiaceae)	4771			1	X
<i>Ceroplastes mosqueras</i> Ben-Dov, 1993 ²	Nar	<i>Solanum betaceum</i> (Solanaceae)	4931			10	X
<i>Coccus hesperidum</i> (Linnaeus, 1758)	Ant	<i>Hibiscus</i> sp. (Malvaceae),	4848			4	X
<i>Coccus</i> sp.	Cal, Tol	<i>Coffea arabica</i> (Rubiaceae)	3498 4888			7	X
<i>Coccus viridis</i> (Green, 1889)	Ant, Cal, Cau, Ris, Tol	<i>Coffea arabica</i> , <i>Faramea</i> sp., <i>Ixora coccinea</i> (Rubiaceae); <i>Cestrum nocturnum</i> (Solanaceae)	3497			33	X
<i>Hemilecanium guanabana</i> Kondo & Hodgson, 2013	VdC	<i>Annona muricata</i> (Annonaceae)	4939			1	X
<i>Philephedra tuberculosa</i> Nakahara & Gill, 1985	Tol	<i>Gossypium</i> sp. (Malvaceae)	4948			9	X
<i>Protopulvinaria longivalvata</i> Green, 1909 ²	Caq	<i>Capsicum</i> sp. (Solanaceae)	4962			10	X
<i>Protopulvinaria pyriformis</i> (Cockerell, 1894)	VdC	Euphorbiaceae	4958			3	X
<i>Pseudokermes vitreus</i> (Cockerell, 1894) ²	Boy, Caq	<i>Ficus</i> sp. (Moraceae)	4965			34	X
<i>Pulvinaria elongata</i> Newstead, 1917	Cal, VdC	<i>Saccharum officinarum</i> (Poaceae)	1507 1836			17	X
<i>Pulvinaria psidii</i> Maskell, 1893	Cun	<i>Coffea arabica</i> (Rubiaceae)	1854			33	X
<i>Saissetia coffeae</i> (Walker, 1852)	Cal, Cun, Qui, Ris	<i>Schinus molle</i> (Anacardiaceae); <i>Tecoma grandis</i> (Bignoniaceae); <i>Coffea arabica</i> (Rubiaceae)	873 3524			66	X

SPECIES	LOCALITY	HOST	CAT	HTY	PTY	SPCM (♀♀ adults)	LV
<i>Saissetia</i> sp.	Cun	<i>Ficus andicola</i> (Moraceae)	824			1	
<i>Tillancoccus koreguaje</i> Caballero & Ramos, 2017	Caq	<i>Saccharum officinarum</i> (Poaceae)	836	X	X	3	
<i>Toumeyella coffeae</i> Kondo, 2013	Cau, NdS, VdC	<i>Coffea arabica</i> (Rubiaceae)	1412 4641			45	X
<i>Toumeyella pini</i> King, 1901	Ind (USA)	<i>Pinus silvestris</i> (Pinaceae)	1510			5	X
Dactylopiidae							
<i>Dactylopius</i> sp.	Cun	<i>Opuntia</i> sp. (Cactaceae)	5537			2	X
Diaspididae							
<i>Aonidiella comperei</i> McKenzie, 1937	Tol	<i>Citrus aurantifolia</i> (Rutaceae)	1837			42	X
<i>Aonidiella orientalis</i> (Newstead, 1894)	Atl, Cau	<i>Nerium oleander</i> (Apocynaceae); <i>Citrus limon</i> (Rutaceae)	4845			8	X
<i>Aspidiotus destructor</i> Signoret, 1869	Ant	<i>Musa</i> sp. (Musaceae)	4846			19	X
<i>Chrysomphalus dictyospermi</i> (Morgan, 1889) ²	Cun	<i>Callistemon</i> sp. (Myrtaceae)	4847			7	X
<i>Diaspis boisduvalii</i> (Signoret, 1869)	Ant, VdC	<i>Musa</i> sp. (Musaceae)	4849 4932			20	X
<i>Duplachionaspis divergens</i> (Green, 1899)	Met, Ris	<i>Saccharum officinarum</i> (Poaceae)	667 4852			11	X
<i>Hemiberlesia cyanophylli</i> (Signoret, 1869) ²	Cun	<i>Liriope</i> sp. (Liliaceae)	4861			15	X
<i>Hemiberlesia rapax</i> (Comstock, 1881)	Cun	<i>Callistemon</i> sp. (Myrtaceae)	4938			3	X
<i>Hemiberlesia</i> sp.	Cal	<i>Coffea arabica</i> (Rubiaceae)	4573			1	
<i>Ischnaspis longirostris</i> (Signoret, 1882)	Ant	<i>Cocos nucifera</i> (Arecaceae)	1010 4940			11	X
<i>Lepidosaphes beckii</i> (Newman, 1869) ²	VdC	<i>Gossypium</i> sp. (Malvaceae)	4942			7	X
<i>Melanaspis</i> sp.	Ant, Cun	<i>Arbutus unedo</i> (Ericaceae); <i>Phormium tenax</i> (Asphodelaceae)	1501 1502			13	X
<i>Odonaspis</i> sp.	Ant	<i>Coffea arabica</i> (Rubiaceae)	4629			3	X
<i>Pseudoparlatoria bennetti</i> (Williams, 1969)	VdC	<i>Veitchia merrillii</i> , <i>Cocos nucifera</i> , <i>Elaeis oleifera</i> x <i>Elaeis guineensis</i> (Arecaceae)	1504			32	X
<i>Parlatoria ziziphi</i> (Lucas, 1853)	Atl	<i>Citrus</i> sp. (Rutaceae)	1885			15	X
<i>Pinnaspis aspidistrae</i> (Signoret, 1869)	Tol	<i>Annona muricata</i> (Annonaceae)	1863			15	X
<i>Pinnaspis buxi</i> (Bouché, 1851)	Ant	<i>Monstera deliciosa</i> (Araaceae)	1864			3	X

SPECIES	LOCALITY	HOST	CAT	HTY	PTY	SPCM (♀♀ adults)	LV
<i>Pinnaspis strachani</i> (Cooley, 1898)	Cal, Suc, Tol	<i>Gossypium</i> sp. (Malvaceae); <i>Saccharum officinarum</i> (Poaceae)	676 4947			25	X
<i>Pseudaonidia trilobitiformis</i> (Green, 1896)	Atl, Bol	<i>Nerium oleander</i> (Apocynaceae)	4960			18	X
<i>Pseudaulacaspis pentagona</i> (Targioni Tozzetti, 1886)	NdS	<i>Passiflora edulis</i> (Passifloraceae)	4956			8	X
<i>Pseudoparlatoria parlatorioides</i> (Comstock, 1883) ²	Cun	<i>Yucca elephantipes</i> (Asparagaceae)	1506			9	X
<i>Pseudoparlatoria suelda</i> Wolff, 2001 ²	Ris	<i>Persea americana</i> (Lauraceae)	4964			4	X
<i>Unaspis citri</i> (Comstock, 1883) ²	VdC	<i>Gossypium</i> sp. (Malvaceae)	4971			2	X
Eriococcidae							
<i>Acanthococcus mokanae</i> González, Ramos & Caballero, 2019	Atl	<i>Hibiscus</i> sp. (Malvaceae); <i>Capsicum</i> sp. (Solanaceae)	4928	X	X	41	X
<i>Uhleria araucariae</i> (Maskell, 1879)	Cun	<i>Araucaria heterophylla</i> (Araucariaceae); <i>Cryptomeria japonica</i> (Cupressaceae)	1876			16	X
Margarodidae							
<i>Eurhizococcus colombianus</i> Jakubski, 1965 ²	Cun	<i>Aloe vera</i> (Asphodelaceae); <i>Coffea arabica</i> (Rubiaceae)	890 4629			2	X
Monophlebidae							
<i>Crypticerya abrahami</i> (Newstead, 1917)	VdC	<i>Annona muricata</i> (Annonaceae)	1858			2	X
<i>Crypticerya brasiliensis</i> (Hempel, 1900) ²	Boy, ASP	<i>Mangifera indica</i> (Anacardeaceae); <i>Psidium guineense</i> (Myrtaceae)	819 1857			12	X
<i>Crypticerya genistae</i> (Hempel, 1912)	Atl, VdC	<i>Arachis pintoi</i> (Fabaceae)	1856			6	X
<i>Crypticerya multicatrices</i> (Kondo & Unruh, 2009) ²	Cun	<i>Citrus sinensis</i> (Rutaceae)	1859			3	X
<i>Laurencella colombiana</i> Foldi & Watson, 2001	Cun	<i>Persea americana</i> (Lauraceae)	4941			8	
Ortheziidae							
<i>Insignorthezia insignis</i> (Browne, 1887)	Chi (Mex); Ant, Cau, Qui, Ris	<i>Coffea arabica</i> (Rubiaceae)	1499 4574			52	X
<i>Mixorthezia minima</i> Konczné Benedicty & Kozár, 2004	Chi (Mex); NdS	<i>Coffea arabica</i> (Rubiaceae)	1806 1862			6	X
<i>Mixorthezia neotropicalis</i> (Silvestri, 1924)	Tol	<i>Coffea arabica</i> (Rubiaceae)	4774			1	
Pseudococcidae							
<i>Antonina graminis</i> (Maskell, 1897)	Cor, Met	Poaceae	4929			25	X
<i>Chorizococcus caribaeus</i> Williams & Granara de Willink, 1992	Cal	<i>Coffea arabica</i> (Rubiaceae)	3495			4	

SPECIES	LOCALITY	HOST	CAT	HTY	PTY	SPCM (♀♀ adults)	LV
<i>Dysmicoccus boninsis</i> (Kuwana, 1909)	Ant, Boy, Cho, Tol	<i>Saccharum officinarum</i> (Poaceae)	843			57	X
<i>Dysmicoccus brevipes</i> (Cockerell, 1893)	Ant, Cal, Cau, NdS, Qui, Ris, Tol, VdC	<i>Cyperus</i> sp. (Cyperaceae); <i>Musa acuminata</i> (Musaceae); <i>Coffea arabica</i> (Rubiaceae);	830 1390 3500 4622 4853			269	X
<i>Dysmicoccus caribensis</i> Granara de Willink, 2009	Cal, Hui. NdS, Qui, Tol, VdC	<i>Coffea arabica</i> (Rubiaceae)	1391			166	X
<i>Dysmicoccus</i> complex <i>joannesi-ae-neobrevipes</i>	Cau, Tol	<i>Coffea arabica</i> (Rubiaceae)	4643 4854			9	X
<i>Dysmicoccus</i> complex <i>texensis-neobrevipes</i>	Ant, Cal, Cau, Hui, Qui, Ris, Tol, VdC	<i>Coffea arabica</i> (Rubiaceae)	1398 3785 4934			510	X
<i>Dysmicoccus grassii</i> (Leonardi, 1913)	Cau, NdS, Qui, Tol	<i>Coffea arabica</i> (Rubiaceae)	4626 4777			13	X
<i>Dysmicoccus mackenziei</i> Beardsley, 1965	Cal, Hui	<i>Coffea arabica</i> (Rubiaceae)	3787 4933			4	X
<i>Dysmicoccus neobrevipes</i> Beardsley, 1959	Ant, Cal, Cau, Qui, Ris, VdC	<i>Coffea arabica</i> (Rubiaceae)	1394 3786 4570			233	X
<i>Dysmicoccus perotensis</i> Granara de Willink, 2009	Cal, Cau	<i>Coffea arabica</i> (Rubiaceae)	4769			4	X
<i>Dysmicoccus quercicolus</i> (Ferris, 1918)	Cal, Cau	<i>Coffea arabica</i> (Rubiaceae)	4624			5	X
<i>Dysmicoccus radialis</i> (Green, 1933)	Qui, Ris	<i>Coffea arabica</i> (Rubiaceae)	4572			13	X
<i>Dysmicoccus</i> sp.	Cun, NdS, Ris	<i>Coffea arabica</i> (Rubiaceae)	1398 4628			6	X
<i>Dysmicoccus sylvarum</i> Williams & Granara de Willink, 1992	Cal, Cau, Tol	<i>Coffea arabica</i> (Rubiaceae)	3787 4627			32	X
<i>Dysmicoccus texensis</i> (Tinsley, 1900)	Chi (Mex); VdC	<i>Coffea arabica</i> (Rubiaceae)	1397 1496			23	X
<i>Dysmicoccus varius</i> Granara de Willink, 2009	Ant, Cal, Cau, NdS, Tol	<i>Coffea arabica</i> (Rubiaceae)	1393 1395 4571			158	X
<i>Ferrisia dasyliirii</i> Kaydan & Gullan, 2012 ²	Ant, Atl, Cor, Suc, Tol, VdC	<i>Mangifera indica</i> , <i>Spondias</i> sp. (Anacardiaceae); <i>Amaranthus</i> sp. (Amaranthaceae); <i>Gossypium</i> sp. (Malvaceae); <i>Musa</i> sp. (Musaceae)	1860			161	X
<i>Ferrisia kondoi</i> Kaydan & Gullan, 2012 ²	Caq, Hui	<i>Licania tomentosa</i> (Chrysobalanaceae); <i>Theobroma cacao</i> (Malvaceae)	1834			5	X
<i>Ferrisia</i> sp.	Cor	<i>Gossypium</i> sp. (Malvaceae)	4936			3	
<i>Ferrisia uzimuri</i> Kaydan & Gullan, 2012	Tol	<i>Coffea arabica</i> (Rubiaceae)	4776			1	

SPECIES	LOCALITY	HOST	CAT	HTY	PTY	SPCM (♀♀ adults)	LV
<i>Ferrisia williamsi</i> Kaydan & Gullan, 2012 ²	Ant, Cun, Caq	<i>Tecoma</i> sp. (Bignonia- ceae); <i>Theobroma cacao</i> (Malvaceae)	4935		X	25	X
<i>Leptococcus neotropicus</i> (Wil- liams & Granara de Willink, 1992)	Caq, Mag	<i>Mangifera indica</i> (Anacar- diaceae); <i>Ficus</i> sp. (Mo- raceae)	1500 4945			19	X
<i>Maconellicoccus hirsutus</i> (Green, 1908)	Ant, Atl	<i>Mangifera indica</i> (Ana- cardiaceae); <i>Lagerstroee- mia speciosa</i> (Lythraceae)	4943			11	X
<i>Macrocepococcus loranthi</i> Morrison, 1919	VdC	¿?	4944			15	X
<i>Paraputo</i> sp.	Cau	<i>Coffea arabica</i> (Rubia- ceae)	4631			13	
<i>Phenacoccus dearnessi</i> King, 1901	Ind (USA)	¿?	1503			5	
<i>Phenacoccus hurdi</i> McKenzie, 1964 ^{1,2}	Cun	<i>Lantana camara</i> (Verbe- naceae)	1505			10	X
<i>Phenacoccus madeirensis</i> Green, 1923	San	Myrtaceae	4952			8	X
<i>Phenacoccus parvus</i> Morrison, 1924	Ant	<i>Coffea arabica</i> (Rubia- ceae)	4632			2	
<i>Phenacoccus sisalanus</i> Granara de Willink, 2007	Ant, Cal, Qui, Ris, VdC	<i>Coffea arabica</i> (Rubia- ceae)	1402 3508			99	X
<i>Phenacoccus solani</i> Ferris, 1918	Ant, Cal, Cau, Qui, Ris, Tol, VdC	<i>Coffea arabica</i> (Rubia- ceae)	1404 3507			71	X
<i>Planococcus</i> complex <i>citri-minor</i>	Cal; Rom (ITA)	<i>Coffea arabica</i> (Rubia- ceae); <i>Populus</i> sp. (Sali- caceae)	3788 4955			10	X
<i>Planococcus halli</i> Ezzat & McCon- nell, 1956 ²	Ant	<i>Lagerstroemia speciosa</i> (Lythraceae)	4959			6	X
<i>Planococcus minor</i> (Maskell, 1897)	VdC	<i>Coffea arabica</i> (Rubia- ceae)	1403			1	X
<i>Planococcus</i> sp.	Cas	<i>Coffea arabica</i> (Rubia- ceae)	4954			5	X
<i>Pseudococcus calceolariae</i> (Lidgett, 1898) ²	Cun	<i>Tecoma</i> sp. (Bignonaceae); <i>Ficus americana</i> (Mora- ceae); <i>Callistemon</i> sp., <i>Syzygium paniculatum</i> , (Myrtaceae); <i>Retrophyllum</i> <i>rospiglosii</i> (Podocarpace- ae); <i>Prunus persica</i> (Ro- saceae)	1877			38	X
<i>Pseudococcus elisae</i> Borchsenius, 1947	Ant, Cal, Cau, NdS Qui, Ris, Tol, VdC	<i>Musa</i> sp. (Musaceae); <i>Cof- fea arabica</i> (Rubiaceae)	1405 3512			404	X
<i>Pseudococcus jackbeardsleyi</i> Gim- pel & Miller, 1996	Ant, Cal, Cau, Cor, Qui, Ris, Suc	<i>Spondias</i> sp. (Anacardi- aceae); <i>Gossypium</i> sp. (Malvaceae); <i>Musa</i> sp. (Musaceae); <i>Coffea arabi- ca</i> (Rubiaceae),	3513			53	X

SPECIES	LOCALITY	HOST	CAT	HTY	PTY	SPCM (♀♀ adults)	LV
<i>Pseudococcus landoi</i> (Balachowsky, 1959)	Ant, Cal, Qui, Ris, Tol, VdC	<i>Coffea arabica</i> (Rubiaceae)	1406 3510			100	X
<i>Pseudococcus longispinus</i> (Targioni Tozzetti, 1867) ²	Cun	<i>Cyclamen persicum</i> (Primulaceae)	825 4961			13	X
<i>Pseudococcus</i> sp.	Cau, Cor, Tol	<i>Ocimum basilicum</i> (Lamiaceae); <i>Gossypium</i> sp. (Malvaceae); <i>Coffea arabica</i> (Rubiaceae)	4634 4635 4775 4953 4957			23	X
<i>Saccharicoccus sacchari</i> (Cockerell, 1895)	Cau, Put, Tol	<i>Saccharum officinarum</i> (Poaceae)	835			112	X
<i>Spilococcus mamillariae</i> (Bouche, 1844)	Cun, Qui	<i>Mammillaria</i> sp. (Cactaceae), <i>Coffea arabica</i> (Rubiaceae)	1509 4772			36	X
<i>Spilococcus pressus</i> Ferris, 1950	Cau, Ris	<i>Coffea arabica</i> (Rubiaceae)	4640			1	X
Putoidae							
<i>Puto barberi</i> (Cockerell, 1895)	Ant, Cal, Cas, Cau, Hui, Nar, NdS, Qui, Ris, San, Tol, VdC	<i>Hibiscus</i> sp. (Malvaceae); <i>Coffea arabica</i> (Rubiaceae)	838 1408			1046	X
<i>Puto antioquensis</i> (Murillo, 1931)	Nar	¿?	4963			1	X
<i>Puto mexicanus</i> (Cockerell, 1893) ^{1,2}	Boy	<i>Quercus humboldtii</i> (Fagaceae)	5538			3	X
Rhizoecidae							
<i>Capitisetella migrans</i> (Green, 1933) ²	Ant	<i>Musa acuminata</i> (Musaaceae)	1855			1	X
<i>Coccidella ecuadorina</i> Konczné Benedicty y Foldi, 2004	Cau, Cun, Nar	<i>Coffea arabica</i> (Rubiaceae)	4620			3	X
<i>Coccidella</i> sp.	Ant, Cun, Nar	Bryophyta; <i>Sonchus oleraceus</i> , <i>Sonchus</i> sp. (Asteraceae); <i>Sida acuta</i> (Malvaceae); <i>Oxalis corniculata</i> (Oxalidaceae), <i>Pennisetum clandestinum</i> (Poaceae), <i>Rumex acetosella</i> (Polygonaceae); <i>Coffea arabica</i> (Rubiaceae)	3496			36	X
<i>Geococcus coffeae</i> Green, 1933 ²	Ant, Cal, Cau, Cun, Nar, NdS, Qui, Ris, Tol, VdC	<i>Galinsoga parviflora</i> (Asteraceae); <i>Crocasmia</i> sp. (Iridaceae); <i>Musa acuminata</i> (Musaceae); Poaceae; <i>Coffeae arabica</i> (Rubiaceae),	1400 1498 3504 4937			966	X
<i>Geococcus johorensis</i> Williams, 1969 ^{1,2}	Ant	<i>Musa acuminata</i> (Musaaceae)	1861			44	X
<i>Neochavesia caldasiae</i> (Balachowsky, 1957)	Ant, Cal, Ris, VdC	<i>Coffeae arabica</i> (Rubiaceae)	1401 3505			65	X
<i>Neochavesia eversi</i> (Beardsley, 1970)	Cun, Tol	Cyperaceae, Poaceae	831			18	X

SPECIES	LOCALITY	HOST	CAT	HTY	PTY	SPCM (♀♀ adults)	LV
<i>Pseudorhizoecus bari</i> Caballero & Ramos, 2018	NdS	<i>Coffeae arabica</i> (Rubiaceae)	1807	X	X	6	X
<i>Pseudorhizoecus proximus</i> Green, 1933	Chi (MEX)	<i>Coffeae arabica</i> (Rubiaceae)	1875			7	X
<i>Rhizoecus americanus</i> (Hambleton, 1946)	Ant, Cau, NdS, Qui, Ris, VdC	<i>Coffeae arabica</i> (Rubiaceae)	1326 4576 4637			34	X
<i>Rhizoecus arabicus</i> Hambleton, 1976	Ant, Cal, Cau, Cun, Qui, Ris, Tol	<i>Musa acuminata</i> (Musaaceae); <i>Coffeae arabica</i> (Rubiaceae)	484			129	X
<i>Rhizoecus atlanticus</i> (Hambleton, 1946)	Ris	<i>Coffeae arabica</i> (Rubiaceae)	4638			3	
<i>Rhizoecus cacticans</i> (Hambleton, 1946) ²	Ant, Boy, Cal, Cau, Cun, Nar, Ris, Tol	Bryophyta; <i>Oreopanax floribundus</i> (Araliaceae); <i>Conyza</i> sp., <i>Chrysanthemum</i> sp., <i>Galinsoga parviflora</i> , <i>Hypochaeris</i> sp., <i>Sonchus oleraceous</i> , <i>Taraxacum officinale</i> (Asteraceae); <i>Tradescantia gracilis</i> (Commelinaceae); <i>Ipomoea</i> sp. (Convolvulaceae); <i>Cyperus</i> sp. (Cyperaceae); <i>Trifolium pratense</i> , <i>Trifolium repens</i> (Fabaceae); <i>Crocasmia</i> sp. (Iridaceae); <i>Sida acuta</i> (Malvaceae); <i>Oxalis corniculata</i> , <i>Oxalis</i> sp. (Oxalidaceae); <i>Bromus</i> sp., <i>Cynodon dactylon</i> , <i>Dactylis glomerata</i> , <i>Eleusine indica</i> , <i>Holcus lanatus</i> , <i>Lolium</i> sp., <i>Pennisetum clandestinum</i> (Poaceae); <i>Polygonum nepalense</i> , <i>Rumex acetosella</i> , <i>Rumex crispus</i> (Polygonaceae); <i>Coffea arabica</i> , <i>Richardia scabra</i> (Rubiaceae); <i>Lantana camara</i> (Verbenaceae), <i>Commelina diffusa</i> (Commelinaceae); <i>Cyperus ferax</i> (Cyperaceae); <i>Musa acuminata</i> (Musaceae); <i>Paspalum notatum</i> (Poaceae); <i>Coffea arabica</i> , <i>Spermacoce alata</i> (Rubiaceae)	483 3518			220	X
<i>Rhizoecus caladii</i> Green, 1933	Ant, Cal, Cun	<i>Coffea arabica</i> , <i>Spermacoce alata</i> (Rubiaceae)	1495 4577 4966			9	X
<i>Rhizoecus coffeae</i> Laing, 1925	NdS	<i>Coffea arabica</i> (Rubiaceae)	1409				

SPECIES	LOCALITY	HOST	CAT	HTY	PTY	SPCM (♀♀ adults)	LV
<i>Rhizoecus colombiensis</i> Ramos & Caballero, 2016	Ant, Cal, Cau, Nar, Qui, Ris, Tol, VdC	<i>Bidens pilosa</i> , <i>Emilia sonchifolia</i> , <i>Erigeron bonariensis</i> , <i>Galinsoga parviflora</i> (Asteraceae); <i>Cyperus ferax</i> (Cyperaceae); <i>Equisetum</i> sp. (Equisetaceae); <i>Crocasmia</i> sp. (Iridaceae); <i>Cuphea lanceolata</i> (Lythraceae); <i>Musa acuminata</i> (Musaceae); <i>Eleusine indica</i> , <i>Holcus</i> sp., <i>Panicum maximum</i> , <i>Paspalum notatum</i> , <i>Pennisetum clandestinum</i> (Poaceae); <i>Plantago major</i> (Plantaginaceae)	678 3519	X	X	494	X
<i>Rhizoecus compotor</i> Williams & Granara de Willink, 1992	Ris	<i>Coffea arabica</i> (Rubiaceae)	4578			6	
<i>Rhizoecus cyperalis</i> (Hambleton, 1946) ²	Cun	<i>Thymus vulgaris</i> (Lamiaceae); <i>Rosa</i> sp. (Rosaceae)	488			23	X
<i>Rhizoecus mayanus</i> (Hambleton, 1946)	Cal	<i>Coffea arabica</i> (Rubiaceae)	3522			1	
<i>Rhizoecus neostangei</i> Miller & McKenzie, 1971	Chi (MEX)	Poaceae	1508			1	
<i>Rhizoecus setosus</i> (Hambleton, 1946)	Cau, Cun, Ris, Tol	<i>Archontophoenix cunninghamiana</i> (Arecaceae); <i>Coffea arabica</i> (Rubiaceae)	4579			75	X
<i>Rhizoecus spenipes</i> (Hambleton, 1946)	Ant, Cal, Qui, Ris, Tol	<i>Coffea arabica</i> (Rubiaceae)	3521			58	X
<i>Rhizoecus stangei</i> McKenzie, 1962	Tol	<i>Coffea arabica</i> (Rubiaceae)	4773			2	X
<i>Rhizoecus variabilis</i> Hambleton, 1978	Ant, Cal, Cun, Qui, Tol	<i>Cuphea lanceolata</i> (Lythraceae); <i>Coffea arabica</i> (Rubiaceae)	4580			34	X
<i>Ripersiella andensis</i> (Hambleton, 1946)	Ant, Cal, Qui, Ris, Tol, VdC	<i>Coffea arabica</i> (Rubiaceae)	1411 3523 4636			145	X
<i>Ripersiella campestris</i> Hambleton, 1946	Chi (MEX)	Poaceae, <i>Coffea arabica</i> (Rubiaceae)	1497			10	X
<i>Ripersiella kelloggi</i> Ehrohn & Cockerell, 1901	Cun	¿?	489			6	X
<i>Williamsrhizoecus coffeae</i> Caballero & Ramos, 2018	Ant; Chi (MEX)	<i>Coffea arabica</i> (Rubiaceae)	4642 4639	X		18	X

Abbreviations: Cat. N° (catalogue number); Ant (Antioquia), ASP (The San Andres, Providencia and Santa Catalina Archipelago), Atl (Atlántico), Boy (Boyacá), Cal (Caldas), Caq (Caquetá), Cas (Casanare), Cau (Cauca), Cho (Chocó), Cor, (Córdoba), Cun (Cundinamarca), Hui (Huila), Mag (Magdalena), Met (Meta), Nar (Nariño), NdS (Norte de Santander), Put (Putumayo), Qui (Quindio), Ris (Risaralda), San (Santander) Suc (Sucre), Tol (Tolima), VdC (Valle del Cauca); ITA (Italy), Rom (Roma); MEX (Mexico), Chi (Chiapas); USA (United States of America), Ind (Indiana); ¿? (No information); ¹New country record, ²New host record (scientific names underline); HTY holotype; PTY paratype; N° SPCM number of mounting-slide specimens; LV Liquid voucher available.

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Scientific note[urn:lsid:zoobank.org:pub:63B566ED-656E-4F86-B173-3C0576114EFF](https://zoobank.org/pub/63B566ED-656E-4F86-B173-3C0576114EFF)**Crossing the Weber Line:
First record of the Giant Bluetongue Skink *Tiliqua gigas* (Schneider, 1801)
(Squamata: Scincidae) from Sulawesi, Indonesia****Thore Koppetsch^{1,*}, Letha L. Wantania², Farnis B. Boneka³ & Wolfgang Böhme⁴**^{1,4}*Herpetology Section, Zoologisches Forschungsmuseum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany*^{2,3}*Department of Fisheries and Marine Science, Universitas Sam Ratulangi, Manado, North Sulawesi, Indonesia***Corresponding author: Email: t.koppetsch@leibniz-zfmk.de*¹[urn:lsid:zoobank.org:author:6028DD4F-017F-4A42-A3A2-621993201402](https://zoobank.org/author/6028DD4F-017F-4A42-A3A2-621993201402)²[urn:lsid:zoobank.org:author:C18E09B6-D0C1-43C3-A64C-12C1B6509F55](https://zoobank.org/author/C18E09B6-D0C1-43C3-A64C-12C1B6509F55)²[urn:lsid:zoobank.org:author:D7CFFB56-9D50-4A94-BCBD-A06210527235](https://zoobank.org/author/D7CFFB56-9D50-4A94-BCBD-A06210527235)²[urn:lsid:zoobank.org:author:FFAC2972-9F52-404B-BA9C-489C7793FF8D](https://zoobank.org/author/FFAC2972-9F52-404B-BA9C-489C7793FF8D)

Abstract. We report for the first time the Giant Bluetongue Skink *Tiliqua gigas* (Schneider, 1801) from the Indonesian island of Sulawesi. This find constitutes the westernmost record for the species and represents the first record of *Tiliqua* Gray, 1825 from west of the Weber Line and for Wallacea. The possible origin of the specimen found and its taxonomic status are discussed in a biogeographical context.

Key words. New record, Wallacea, Scincidae, *Tiliqua*, Sulawesi, Indonesia, biogeography.

INTRODUCTION

Bluetongue skinks of the genus *Tiliqua* Gray, 1825 are exceptional large representatives of the Scincidae, one of the most diverse lizard families with nearly 1700 species described (Uetz et al. 2020). They are well-known for stretching out their bright blue to blackish coloured tongue towards potential predators when disturbed, though this behaviour might also serve as intraspecific signaling (Abramjan et al. 2015).

As popular reptiles that often can be found in herpetoculture, bluetongue skinks are of particular interest for the international pet trade (Yuwono 1998; Iskandar & Erdelen 2006; Chng et al. 2016), although they can be easily bred also in captivity (Brauer 1980; Schade 1980; Laphorne & Laphorne 1987; Gassner 2000).

Five of the seven species of *Tiliqua* are distributed in Australia, where they occur in various habitats from arid to humid climate conditions and at different elevations (Shea 2000a). Only two species of bluetongue skinks are found outside of the Australian continent: *Tiliqua gigas* (Schneider, 1801) and *Tiliqua scincoides* (White, 1790) (Hitz & Hauschild 2000).

For a long time all non-Australian bluetongue skinks were assigned to *T. gigas*. However, based on studies by Shea (1992), populations from the Tanimbar and Baber Islands (eastern Lesser Sundas, Indonesia) were found

to be different from *T. gigas* and were described as *Tiliqua scincoides chimaerea* Shea, 2000, i.e., a subspecies of a taxon previously known only from Australia (Shea 2000b). In the southeastern region of Irian Jaya (Merauke) bluetongue skinks with a phenotype sharing characteristics of both *T. gigas* and *T. scincoides* were reported and appear as “Irian Jaya Bluetongue” in the pet trade (Hitz & Hauschild 2000; Noël 2009).

As shown on Figure 1, *T. gigas* has a widespread but fragmented distribution reaching from the eastern parts of New Guinea to eastern Indonesia and being spread over several islands (Shea 2000c).

Within this range three subspecies are distinguished showing differences in head scalation, body size and colouration. Populations found in the Aru and Kei archipelagos (southeastern Maluku Islands, Indonesia) are assigned to the endemic subspecies *Tiliqua gigas keyensis* Oudemans, 1894 (Shea 2000c; Karin et al. 2018). *Tiliqua g. evanescens* Shea, 2000 occurs in southern and eastern New Guinea and also on islands off the north-eastern and eastern coast of New Guinea (Admiralty, D’Entrecasteaux and Trobriand Islands) (Shea 2000c). This subspecies is geographically separated from the northern subspecies *T. g. gigas* by the central New Guinea Highlands and its mountain chains. This biogeographical pattern is also present in other New Guinean reptiles, see, for example, the recent separation of the southern *Crocodylus*

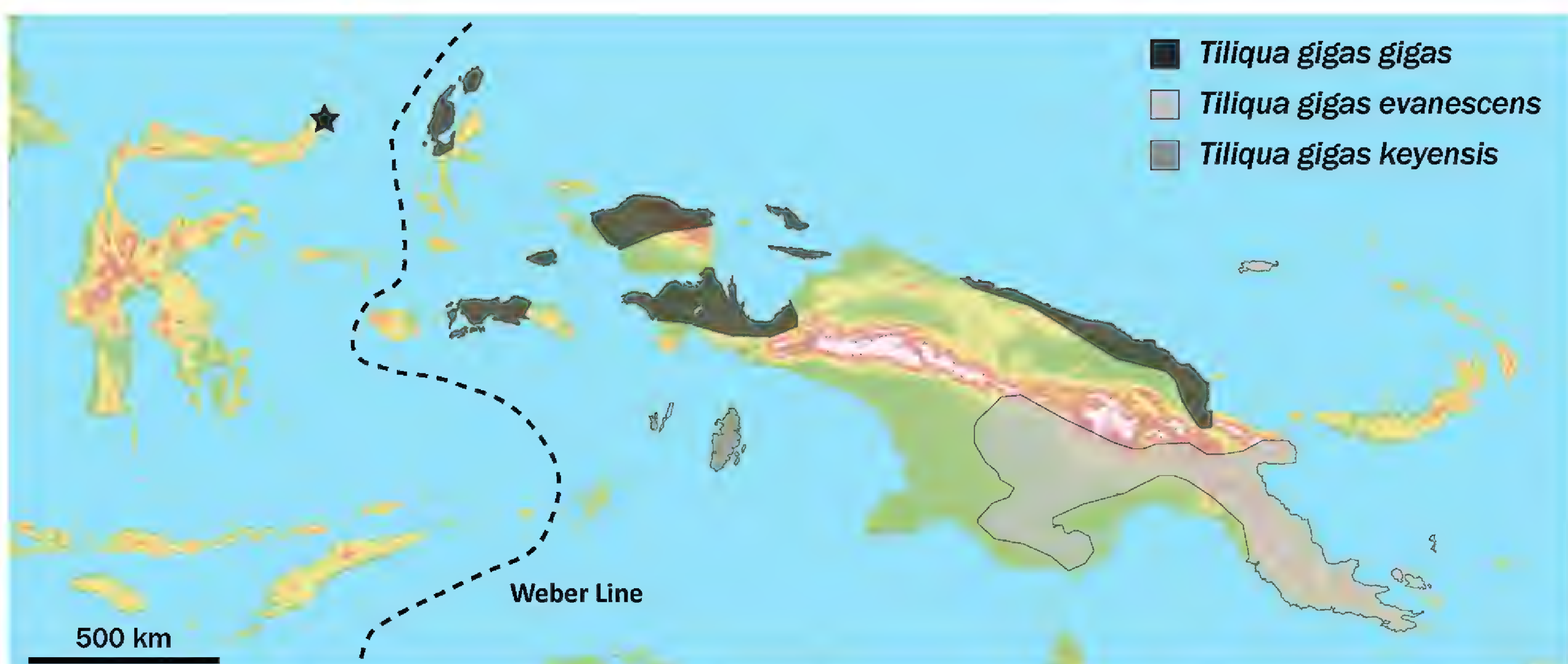


Fig. 1. Distribution map of *Tiliqua gigas* and its subspecies (modified from Shea, 2000c). *T. g. keyensis* is restricted to the Aru and Kei Islands. *T. g. evanescens* is geographically separated from the northern subspecies *T. g. gigas* by the central New Guinea Highlands and its mountain ranges. The black star denotes the new distribution record for Sulawesi, Indonesia.

halli Murray et al., 2019 from the northern populations of *C. novaeguineae* Schmidt, 1928.

Tiliqua g. gigas shows the westernmost distribution of all non-Australian bluetongue skinks with records from the Maluku Islands: Ambon, Halmahera (though not recorded recently by Setiadi & Hamidy [2006]), Misool, Morotai, Saparua, Seram and Ternate, but it can be also found in northern New Guinea and islands along its northern coast (Biak, Doom, Karkar, Seleu, Yapen) (Kopstein 1926; Mys 1988; Shea 1982, 1992, 2000c).

Some old mentions of bluetongue skinks from Java and Sumatra (Boulenger 1887; Duméril & Bibron 1839; Werner 1910) remained unconfirmed and were most likely caused by misidentification of collection data or providing the location of the port of shipment (Shea 2000a).



Fig. 2. Photography of the living specimen of *Tiliqua gigas gigas* found near Airmadidi in Northern Sulawesi, Indonesia.

Apart from those early and doubtful locality data, all reliable and confirmed records of *Tiliqua* are located east of the Weber line (Shea 2000a). Here we report the first record of *T. g. gigas* from Sulawesi, Indonesia (Fig. 2).

MATERIAL AND METHODS

A large scincid lizard was discovered on 6 August 2019 near Airmadidi, Minahasa Utara, North Sulawesi, Indonesia (Fig. 1), where it was kept alive by locals. Airmadidi is a village located southeast and in about 15 kilometers distance to Manado, as well as in proximity to the highest volcano of Sulawesi, Mount Klabat, raising 1,995 meters a.s.l.. This specimen of *T. gigas* had been caught in some distance to the village located nearby in the undergrowth of secondary rainforest at around 215 meters a.s.l.. The habitat was characterized by a dense and flourishing ground vegetation, mainly consisting of creepers (Fig. 3). No streams or pools of water can be found directly near to the collection site. Since bluetongue skinks are partially under a high collection pressure for purposes of pet trade and cases of intense suchlike collection or extirpation had been reported from type or first record localities, for instance in the eublepharid gecko *Goniurosaurus luii* Grismer, Viets & Boyle, 1999 (Lindenmayer & Scheele 2017), we refrain from providing detailed location data, like geographical coordinates. Identification and record are based on the live specimen that was returned to be kept alive in the village after examination.



Fig. 3. Habitat in which *Tiliqua gigas* was found in Northern Sulawesi.

RESULTS AND DISCUSSION

The specimen found can be easily identified as a member of the bluetongue skinks *Tiliqua* due to its characteristic tongue and body colouration, a large body size and compact body shape (Fig. 4). Identification as *T. gigas gigas* could be confirmed by the presence of black, unspotted or slightly spotted limbs, an extensive black-striped and deep orange spotted pattern on the ventral side and blackish edged head scales based on the diagnostic characters presented in Hauschild & Hitz (2000) and Shea (2000c). Moreover, the basic dorsal colouration of the specimen found is dark-reddish brown with ten narrow black transverse bands on the trunk and 14 broad black bands on the tail. It shows an unpatterned and bright orange-coloured throat. In addition, the snout-vent length is about 290 mm, the tail length is 228 mm (measured in the field by one of the authors).

Habitus and size of the specimen resembles specimens from the northern Maluku Islands (Ternate, Halmahera, Misool). Even though this subspecies shows a high degree of variability within in its geographical range (Shea 1992), individuals from the northern Maluku Islands normally have a snout-vent length of more than 270 mm and more darkish colouration (Shea 2000c). In addition,

a dark-striped belly pattern was recorded for most specimens from Halmahera (Shea 2000c).

Bluetongue skinks of the genus *Tiliqua* have never been recorded from Sulawesi before (Iskandar & Tjan 1996; Gillespie et al. 2005; Wanger et al. 2011; Koch 2012). This new record is situated about 250 km distance west of the distribution known so far and expands the distribution range of *T. gigas* from eastern New Guinea to Sulawesi within the Wallacea to about 3.000 km in total. Bluetongue skinks are normally well-known to local people as they are hunted for consumption (Wolter 1980; Shea 2000c). In New Guinea specimens of *Tiliqua* are also known under the local name ‘ular panana’ (‘ular’ = snake; see Kopstein 1926), indicating that they are often mistaken for a snake and thought to be venomous, due to their cylindrical, short-legged appearance and their conspicuous defensive display. However, bluetongue skinks were unknown to the local people at the location where our specimen was found. Therefore, an unintentional introduction by humans has to be taken into account and cannot be ruled out.

The geographically nearest distance to places, where *T. gigas* is recorded from, are in the northern Maluku Islands (Ternate and Halmahera). Nevertheless, these islands are still more than 250 km away from our northern



Fig. 4. Defensive posture of *Tiliqua gigas* from Northern Sulawesi, Indonesia. Note the blueish tongue stretched out towards potential predators.

Sulawesi site. This gap implies a crossing of the biogeographically important Weber Line running east of Sulawesi and separating the Oriental and Oceanian faunas (Weber 1902; Lohman et al. 2011; Holt et al. 2013; Vilhena & Antonelli 2015).

An unintentional introduction by humans via transport in freight and cargo is common in different small-sized skink species (Köhler et al. 1997; Chapple et al. 2015). That is, however, unlikely at least for adult individuals of such a large and conspicuous skink species like *Tiliqua gigas*. Of course this cannot be ruled out completely, since also lizards of larger size have been introduced to islands out of their distribution range, for example, *Agama agama* (Linnaeus, 1758) on islands of Macaronesia, in the Mediterranean Sea or in the Indian Ocean (Wagner et al., 2012). Finally, pet trade for herpetoculture is not widespread especially in rural areas of Sulawesi, since larger reptiles like monitor lizards are caught and kept for consumption. Consequently, escaped specimens from the pet trade are improbable in this case.

An undetected population of *T. gigas* in northern Sulawesi cannot be excluded, since also during intensive herpetological field surveys bluetongue skinks were not observed, even from islands they had been recorded from previously (Setiadi & Hamidy 2006; Karin et al. 2018). Especially skinks are known for their dispersal potential even to islands located away from the coast line of the main land (Adler et al. 1995). Not only small and

inconspicuous lizard species can remain undiscovered for a long time, as shown by recent discoveries of several species of monitor lizards from Indonesian and New Guinean Islands (Ziegler et al. 2007; Weijola et al. 2016; Böhme et al. 2019). Therefore, even such relatively large lizards, like *Tiliqua*, seem to show some potential for new discoveries and unanswered questions like the blue-tongue skinks from Irian Jaya (Hitz & Hauschild 2000; Noël 2009) or the subspecies of *T. gigas* described by Shea (2000b, c).

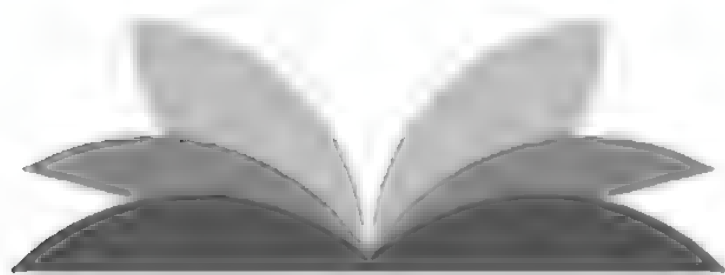
Acknowledgements. The authors thank Dr. Robert Hitz (Thal, Switzerland) for providing comparative photo material of captive-bred *T. gigas* specimens, and Morris Flecks (ZFMK) for assisting in preparing a distribution map. TK is grateful to Dr. Fabian Herder (ZFMK) for the possibility to participate in field work on Sulawesi and to the German Academic Scholarship Foundation for providing a travel grant.

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Research article[urn:lsid:zoobank.org:pub:607B5771-A379-42B6-A9A7-B5D5A2AB27FB](https://zoobank.org/pub:607B5771-A379-42B6-A9A7-B5D5A2AB27FB)**Larval development and morphology of six Neotropical poison-dart frogs
of the genus *Ranitomeya* (Anura: Dendrobatidae)
based on captive-raised specimens****Benjamin Klein¹, Ruth Anastasia Regnet², Markus Krings³ & Dennis Rödder^{4,*}**^{1,2,3,4}*Zoologisches Forschungsmuseum Alexander Koenig, Leibniz Institute for Animal Biodiversity,
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Abstract. Larval development is a crucial step during the ontogeny of amphibians, concomitantly it is the most sensitive life phase in this group. Due to the complex morphological, physiological and anatomical changes, in addition to their susceptibility to the environment changes, this phase is known as one of the most critical period of development as well as an obstacle in ex-situ breeding programs. Tadpole growth rates can be used to predict the effects of biotic interactions, as well as to predict the survival rate on environmental changes. The assessment of the mortality rate during this phase can be performed using a non-invasive image-based tool, programmed on the open source statistical platform R, SAISAQ (semi-automatic quantification of image-based surface area). It allows analyzing semi-automatically a sequence of standardized image files in order to quantify growth rates. However, the current literature lacks estimates of the larval growth rates for the most species of amphibians, which is also true for species of the genus *Ranitomeya* Bauer, 1986. Herein, we present the data of the complete larval development of *Ranitomeya amazonica* (Schulte, 1999), *R. benedicta* Brown, Twomey, Pepper & Sanchez-Rodriguez, 2008, *R. imitator* (Schulte, 1986), *R. reticulata* (Boulenger, 1884), *R. sirensis* (Aichinger, 1991) and *R. vanzolinii* (Myers, 1982), assisted by photographs, drawings and tables with detailed information about the metamorphosis. In addition, we provide a new larval description for *R. benedicta*. The results presented here also provide new data of the larval development and morphology for the target species, based on a sample series for each species. With this information, we want to contribute to a better understanding of the group and provide important data to help solve the systematic relationships puzzle. Providing also a baseline to improve further research on captive breeding, our results may have important implications for conservation breeding programs.

Keywords. Amazon, conservation, ex-situ, *Ranitomeya benedicta*, SAISAQ, tadpole.

Resumen. El desarrollo larvario es un periodo crucial en la ontogenia de los anfibios y al mismo tiempo la fase más sensible de la vida de este grupo. Debido a los complejos cambios morfológicos, fisiológicos y anatómicos, además de la susceptibilidad a los cambios ambientales, esta fase es conocida como uno de los periodos más críticos de desarrollo así como un obstáculo en los programas de reproducción ex-situ. Las tasas de crecimiento de los renacuajos pueden ser empleadas para predecir los efectos de las interacciones bióticas, así como predecir la tasa de supervivencia de los anfibios a los cambios ambientales. Se puede realizar la evaluación de la tasa de mortalidad de los renacuajos mediante una herramienta no invasiva basada en imágenes, programada en la plataforma estadística de código abierto R, SAISAQ (Semi-Automatic Surface Image-Based Quantification). Por medio de este, es posible obtener una secuencia semi automática de archivos de imagen estandarizados, con el fin de evaluar el crecimiento en relación al tiempo. Sin embargo, la literatura actual presenta una carencia de estimaciones de la tasa de crecimiento basadas en imágenes del desarrollo larvario para la mayoría de las especies de anfibios, algo igualmente observado para las especies del género *Ranitomeya* Bauer, 1986. Así, presentamos aquí los datos del desarrollo larvario completo de *Ranitomeya amazonica* (Schulte, 1999), *R. benedicta* Brown, Twomey, Pepper & Sanchez-Rodriguez, 2008, *R. imitator* (Schulte, 1986), *R. reticulata* (Boulenger, 1884), *R. sirensis* (Aichinger, 1991) y *R. vanzolinii* (Myers, 1982), asistidos por fotografías, ilustraciones y tablas con información detallada acerca de la metamorfosis. Además proporcionamos una descripción larvaria inédita para *R. benedicta*. Los resultados aquí presentados también proporcionan nuevos datos acerca de la morfología y el desarrollo larvario de las especies aquí estudiadas, basados en una serie de muestras para cada especie. Estas informaciones contribuyen para una mejor comprensión del grupo y proporcionan datos importantes para ayudar a resolver el tan complejo rompecabezas de las relaciones sistemáticas. Además promueven una base de conocimiento para futuras investigaciones sobre la cría en cautividad de anfibios, una importante herramienta en los programas de cría en cautividad para la conservación de especies de anfibios amenazadas.

Palabras clave. Amazónia, cría en cautividad, ex situ, renacuajo, *Ranitomeya benedicta*, SAISAQ.

INTRODUCTION

Anurans currently include more than 7,000 described species (Frost 2020) and are by far the most species-rich and evolutionary successful group among the extant amphibians. This evolutionary success is promoted by their wide diversity of survival and reproductive strategies, as well as their life histories (Duellman & Trueb 1986; Wells 2007). The huge variety of functional types, including terrestrial, aquatic, fossorial and arboreal forms and their morphological adaptations allowed anurans to occupy a wide array of terrestrial and fresh-water niches (Duellman & Trueb 1986; Wells 2007). However, due to their thin and permeable skin as well as their ectothermy, they are highly susceptible to humidity and temperature variations, the most important abiotic factors within their habitats (Wells 2007).

Poison-dart frogs belong to the superfamily Dendrobatoidea Cope, 1865 and include about 328 known species divided into the families Aromobatidae and Dendrobatidae (Grant et al. 2006; Brown et al. 2011; Frost 2020). All members have a small to medium size of 2–6 cm snout-vent length (SVL) in combination with a highly complex social and reproductive behavior (Lötters et al. 2007; Brown et al. 2011). The genus *Ranitomeya* Bauer, 1986, which is placed within the family Dendrobatidae, consists of 16 species arranged into four species groups, namely the *R. defleri* Twomey & Brown, 2009, *R. reticulata* (Boulenger, 1884), *R. vanzolinii* (Myers, 1982) and *R. variabilis* (Zimmermann & Zimmermann, 1988) groups (Brown et al. 2011). Species of that genus are characterized by their diminutive size with SVL less than 21 mm, their bright aposematic coloration and an almost smooth to slightly granular dorsal surface (Daly et al. 1987; Vences et al. 2003; Brown et al. 2011). Furthermore, the first finger is reduced and shorter than the second, which is the largest of all four fingers (Brown et al. 2011).

In 2011, Brown et al. published a revision of the genus *Ranitomeya*, which represents the actual and widely accepted classification for this group (e.g., Sánchez 2013; Vargas-Salinas et al. 2014; Krings et al. 2017). Within their study, systematic arrangements and the history of that genus are explained, based on molecular phylogenetics in combination with adult and larval morphology. For understanding the systematic and phylogenetic relationships, it is a general consensus that morphological data is an indispensable tool. Regarding taxonomic and phylogenetical purposes, we cannot neglect the knowledge about the morphology of the amphibian larval phase (i.e., tadpoles), where many of the descriptions of the larval stage are quite incomplete, based on a single sample or data are totally absent.

For the genus *Ranitomeya*, many of the tadpole descriptions are based on back riding tadpoles during the transport by the adults to water bodies (Sánchez 2013).

At this stage of development, the tadpoles often lack fully developed tooth rows or other specific characteristic traits of the species (Brown et al. 2011). Furthermore, clutches of *Ranitomeya* species are very small, which makes it difficult to obtain a larger number of specimens at a time, and tadpoles that have already been carried by adults to a water site where they will develop are hard to find. One way to locate tadpoles at this stage is observing the adults, which are shy and therefore hard to discover (Sánchez 2013). In a captive breeding framework, higher numbers of tadpoles can be analyzed across a long time span making it possible to document the complete development. Furthermore, as conservation breeding becomes more and more important detailed information on developmental rates can be very helpful for ex-situ breeding programs. By optimizing husbandry conditions, potential effects of artificial nutrition and artificial environmental conditions can be minimized, although they may occur. Thus, results obtained from captive bred specimens should be ideally complemented and confirmed by data collected in the field.

The aim of this study is to provide, as accurately as possible, data concerning the complete larval morphology and development of the tadpoles of *Ranitomeya amazonica* (Schulte, 1999), *R. benedicta* Brown, Twomey, Pepper & Rodriguez, 2008, *R. imitator* (Schulte, 1986), *R. reticulata*, *R. sirensis* (Aichinger, 1991) and *R. vanzolinii* based on specimens obtained from captive breeding. In the study by Brown et al. (2011), descriptions of *R. amazonica* tadpoles are presented based on a tadpole in Gosner's stage 29, as well as those of *R. imitator* based on a tadpole in stage 26, of *R. reticulata* based on a tadpole in stage 30 and of *R. vanzolinii* based on a tadpole in stage 38. The tadpole description of *R. benedicta* includes only a mouthpart description which was presented by Brown et al. (2008). As stated by the authors the sample ended up being ruined by the fixation process, making it impossible to describe the tadpole (Brown et al. 2008). The tadpole of *R. sirensis* from the stages 25–36 was described in detail by May et al. (2008a) under the name *Ranitomeya biolat* (Morales, 1992) (c.f. Brown et al. 2011) which is considered to be a synonym of *R. sirensis* (Frost 2020).

We present in this study the first larval description of *R. benedicta* and provide image-based growth rate estimates of larval development for all target species, based on the SAISAQ (Semi Automatic Image based Surface Area Quantification, Kurth et al. 2014) tool. In addition, all data presented herein will contribute to fill knowledge gaps of the amphibian larval development, which is also useful for ex-situ breeding programs, in response to the biodiversity crisis, which requires a moral and ethical obligation for proactive interventionist conservation actions to assist species recovery and reduce the population decline.

MATERIALS AND METHODS

Captive Management and Breeding

Adult specimens of the species *R. amazonica*, *R. benedicta*, *R. imitator*, *R. reticulata*, *R. sirensis* and *R. vanzolinii* were acquired from pet trade and kept in customized terraria at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn, Germany. According to the vendors the specimens were captive bred as F_2 from specimens exported from the countries of origin. Correct taxonomy was confirmed by comparing the external morphology with the respective original descriptions.

For the course of the study, groups of five specimens of *Ranitomeya amazonica*, two specimens of *R. imitator*, two specimens of *R. reticulata*, four specimens of *R. sirensis* and four specimens of *R. vanzolinii* were kept in terraria of 40x50x40 cm, while three specimens of *R. benedicta*, four specimens of *R. imitator* and four specimens of *R. vanzolinii* were kept in terraria of 60x50x50 cm size. *Ranitomeya* individuals did not have contact with other individuals of the other species of the genus, also kept in terrariums, thus avoiding hybridization between species.

Each terrarium was equipped on the base with a filter mat which was covered with local leaf litter. The rear and one of the sides were covered with cork tile (Lucky Reptile®, Schwarzkorkrückwände). Artificial lighting was promoted with a LED light (Solar Stinger, 1100 Sunstrip Dimmable Driver, 25W) and daily, artificial daylight was provided from 8 a.m. to 8 p.m. In addition, the terrarium had a bottom irrigation system, a small body of standing water with a drain in a sieve form, located in one of the front corners of the terrarium and a misting system. The misting system was activating three times a day for 120 seconds, divided into twelve alternating intervals of ten seconds spraying, followed by ten seconds pause. Average air and water temperature fluctuated between 22 and 26 °C.

In order to ensure a finely storied vertical structure and provide opportunities to refuge and breeding sites, the terraria were heavily planted with *Ficus pumila* L., *Scindapsus* sp. as also *Neoregelia* sp. “fireball bromeliad” which provides a natural phytotelm for the anurans, important resource for laying the eggs. Additionally, the micro ambient was equipped with stones, roots and film containers (35mm) thus providing additional artificial phytotelms. The amphibians were fed with a diet of *Drosophila melanogaster* Meigen, 1830 or collembolans, every two to three days, and the food was enriched with vitamins and minerals (Herpetal® Mineral + Vitamin D3, Korvimin ZVT + Reptil).

Detected clutches were removed with aid of water and pipettes and placed into petri dishes. To ensure stable conditions, the clutches were transferred into an environmental test chamber (MLR-352H-PE, Panasonic Bio-

medical Sales Europe BV, Netherlands), which was set to a humidity of 80%, a temperature of 24 °C and a twelve hour photoperiod from 8 a.m. – 8 p.m. Every second day all eggs were wetted, except the clutches of *R. amazonica* which were completely covered with enriched pure water, attending the reproductive behavior of the species, as e.g. mentioned in Poelman & Dicke (2007) and Poelman et al. (2013).

After hatching, the larvae were kept separated within small translucent plastic containers (10x10x10 cm), which were filled with enriched pure water and several oak leaves as well as a stem of *Ceratophyllum demersum*. Each container was placed into the environmental test chamber and got a specific identification number. Every two to three days, two thirds of the water were exchanged, in order to preserve the favorable environment for the tadpole. The larvae were fed with a finely ground ration of several types of algae and fish food *ad libitum*, which is different from the natural food. These species are known for their oophagous and predatory behavior in the natural environment (Lötters 2007; Poelman & Dicke 2007). In addition, specimens could graze on biofilm and algae that naturally grew within their container.

When the forelimbs emerged, a small piece of cork tile was placed on the water surface in order to provide a small “land area”. During the latest steps of metamorphosis, when the tail was resorbed, the froglets were transferred to a new container with a huge “land area”, covered with oak leaves, as well as a small water body (18x13x6 cm). The container was sealed with a perforated cover to ensure air exchange. From this moment, the froglets were fed with a diet of *Drosophila melanogaster* and collembolans.

The climate at each known location of the six different species, as defined by Brown et al. (2011), was obtained using ArcGIS (Environmental Systems Resource Institute, ArcGIS 10.2.2, Redlands, California). In order to do so, the longitudinal and latitudinal values of the locations were received through georeferencing of available distribution maps. On the one hand, these coordinates were used to generate a new map which contains the distribution areas of the study organisms (Fig. 1). Expert range maps provided by IUCN were randomly sampled every 10 km² to estimate annual mean, and monthly minimum and maximum temperatures within the geographic range of each species. Modern climate data with a spatial resolution of 30 arc sec was obtained from the free global online database CHELSA (Karger et al. 2017a, b).

Measurements

During their development, the growth rate of the active and mobile tadpoles was documented using a photo camera (EOS 600D, Canon® Deutschland GMBH, Krefeld, Germany), which was mounted on a table-top tripod in a fixed distance to the object. Photographs were taken

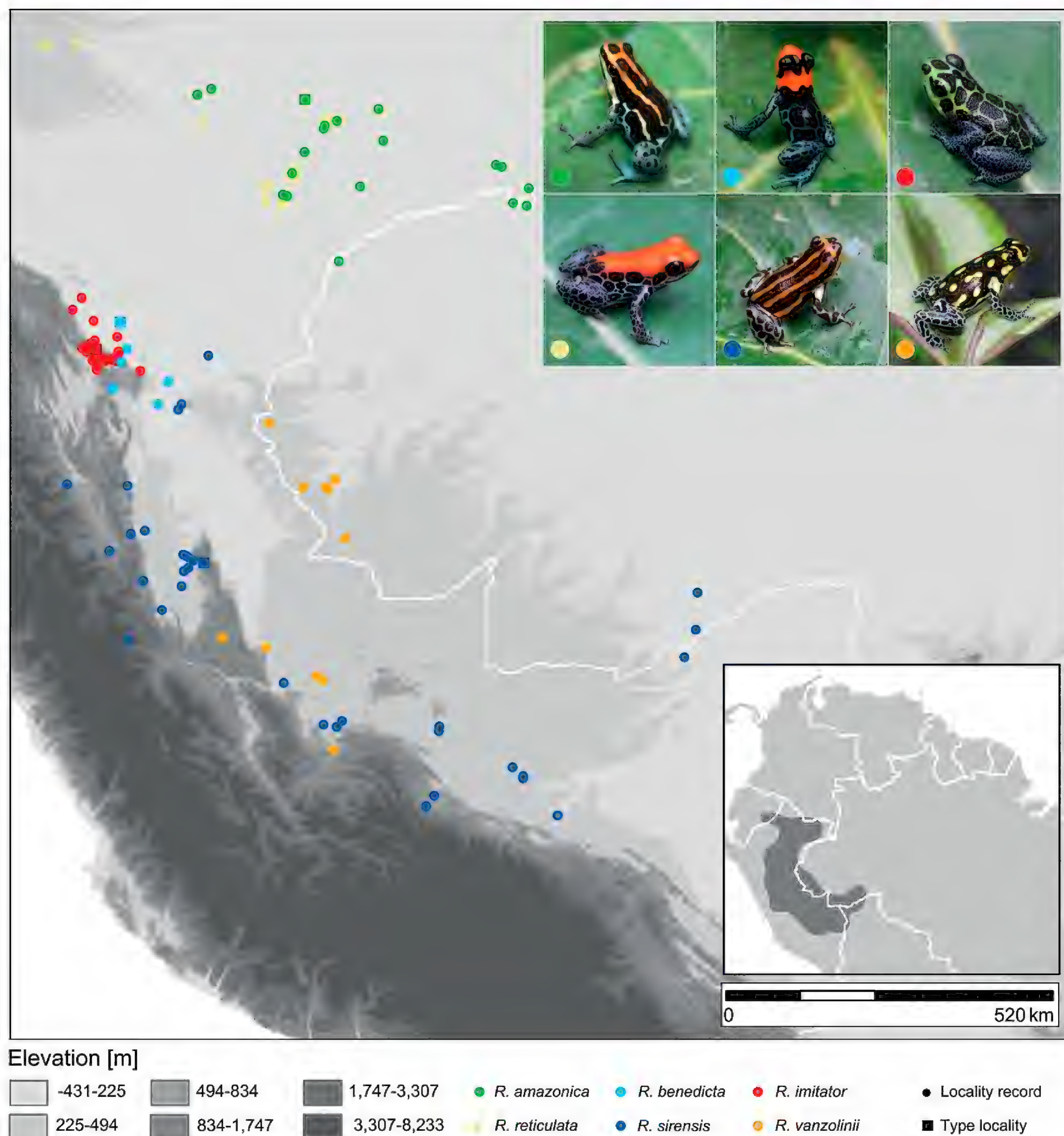


Fig. 1. Known distribution of *Ranitomeya amazonica* (green), *R. benedicta* (light blue), *R. imitator* (red), *R. reticulata* (yellow), *R. sirensis* (blue) and *R. vanzolinii* (orange). Darker shades of gray indicate higher elevations. The inset map displays the distribution of all six compared species, which are shown in the upper right corner of that figure with the corresponding color code.

three times a week, on alternate days. For this purpose, the larvae were placed into a translucent petri dish on top of a light source (CL 6000 LED, Carl Zeiss® Microscopy GMBH, Jena, Germany) which was modified by an alabaster glass. Thus, the light was homogenously distributed and therefore ensured a high contrast between the object and the background.

In all photography sessions, first a standard picture was taken to calibrate an image analysis software programmed in the open source statistics platform R (R Development

Core Team, 2014), which allows a semiautomatic procession of standardized image files (SAISAQ, Kurth et al. 2014). Subsequently the settings and distances were kept constant and all tadpoles were photographed. The software measured the surface area of each tadpole, which is strongly correlated to the body mass. Therefore, a picture series of the same individual documenting its development leads to a graph which represents the growth rate. Every tadpole was photographed with four different settings, ranging in light intensity and different sensitivities

of the camera (Appendix I) which allows observing the tadpole in more details and assisting the software to set the threshold between the object and the background more efficiently. Dorsal and ventral high-resolution pictures, of each tadpole, were created with a special camera setup (Canon EOS 7D mounted on a P-51 Cam-Lift, Dun Inc., Virginia, USA), which perform automatically multiple pictures in different depths and stacks the photos in order to create a final clear image.

Length based measurements were taken to the nearest of 0.1 mm with a stereomicroscope and its integrated eyepiece (Stemi 2000 C, Carl Zeiss® Microscopy GmbH, Jena, Germany) or ImageJ (National Institutes of Health, ImageJ 1.42q, Bethesda, Maryland). The morphological terminology, characters and measurements are determined following McDiarmid & Altig (1999) (Fig. 2) extended by larval measurements from Lavilla & Scrocchi (1986) as cited in Mijares-Urrutia (1998).

Characters and measurements following McDiarmid & Altig (1999; Fig. 2) are: first anterior tooth row (A1); second anterior tooth row (A2); medial gap in first anterior tooth row (A1-GAP); anterior (upper) labium (AL); body length, measured from the tip of the snout to the junction of the posterior body wall with the axis of the tail myotomes (BL); internarial distance, measured between centers of narial apertures (IND); interorbital distance, measured between centers of pupils (IOD); lower jaw sheath (LJ); lateral process of upper jaw sheath (LP); labial tooth row formula (LTRF); mouth (M); marginal papillae (MP); maximum tail height (MTH); oral disc (OD); posterior (lower) labium (PL); first posterior tooth row (P1); second posterior tooth row (P2); third posterior tooth row (P3); medial gap in first posterior tooth row (P1-GAP); tail length (TAL); tail muscle height at base (TMH); tail muscle width at base (TMW); total length (TL); submarginal papillae (SM); upper jaw sheath (UJ).

Characters and measurements following Lavilla & Scrocchi (1986) as cited in Mijares-Urrutia (1998) are: body width at eye level (BWE); body width at nostril level (BWN); horizontal eye diameter (ED); eye nostril distance (END); maximum body height (MBH); maximum body width (MBW); oral disc width (ODW); rostrum-eye distance, from tip of snout to the center of the eye in lateral view (RED); rostrum-nasal distance, from tip of snout to the center of the nostril in lateral view (RND); rostrum-spiracle distance, from tip of snout to center of the spiracle in lateral view (RSD).

Besides that, staging of the development process took place according to Gosner (1960), voucher specimens were euthanized using a saturated solution of Chlorobutanol, subsequently preserved in 6% formalin, and after an ascending alcohol series, preserved in 70% ethanol at the herpetological section of ZFMK. The voucher numbers of each tadpole are provided in the results section. A brief description of the natural history of each species covered in this study can be found in Appendix II.

RESULTS

Species Accounts

Ranitomeya amazonica (Schulte, 1999)

Breeding behavior in captivity. The breeding pairs, among the five specimens of *R. amazonica*, placed the clutches of four to six anthracite eggs in the bromeliad phytotelm. While those egg depositions had no clear frequency, later depositions in a water filled film container occurred every two to five days. Thereby, the clutches were placed directly underneath the water surface of the vertically orientated container, which was placed on the ground next to a large stone. Moreover, at one day a single tadpole at stage 25 was found at the ground of the container, beneath a newly produced clutch.

Larval morphology. The description of the tadpole is based on one specimen at stage 41 (ZFMK 97374). Further voucher specimens are ZFMK 97357, 97362, 97366, 97370–97373. According to McDiarmid & Altig (1999), *R. amazonica* tadpoles belong to the exotrophic, lentic, benthic, arboreal larval type. All measurements that were used to calculate the following proportions and its comparison with the other species of this study, can be found in Appendix III.

Dorsal view: Body shape is oval and moderately elongated ($MBW/BL=0.75$). The snout is short and moderately pointed ($RED/BL=0.23$, $BWN/BWE=0.56$), nares are small and elliptical, positioned dorsally and orientated laterally. Nares are situated closer to snout than to eyes ($RND/RED=0.43$). Eyes are large ($ED/BL=0.12$), positioned dorsally and orientated laterally. Internarial distance is smaller than interorbital distance ($IND/IOD=0.52$). Single, sinistral spiracle is not visible in dorsal view.

Lateral view: Body is depressed ($MBH/MBW=0.59$), snout is rounded. The spiracle is positioned below the longitudinal axis, at the second half of the body ($RSD/BL=0.64$), the inner wall is free from the body, opening is round and the spiracle tube is short. The maximum body height is situated between the eyes and the tail. The tail is long and narrowly rounded ($TAL/BL=1.95$, $TAL/TL=0.66$). The musculature is well developed ($TMH/MTH=0.58$, $TMW/MBW=0.33$). The “V”-shaped myosepta are visible along the whole length of the tail, particularly at the first half. Upper fin originates posterior to the tail-body junction and the margin of the lower fin. Upper fin is slightly higher than the lower fin. Ventral tube is dextral, emergence from abdomen sagittal, opening is rounded. Hindlimbs are fully developed. Oral apparatus is visible in lateral view.

Oral apparatus: Oral disc is elliptical, positioned ventrally and covers nearly one third of the body width ($ODW/MBW=0.27$), emarginated. Marginal, ensiform,

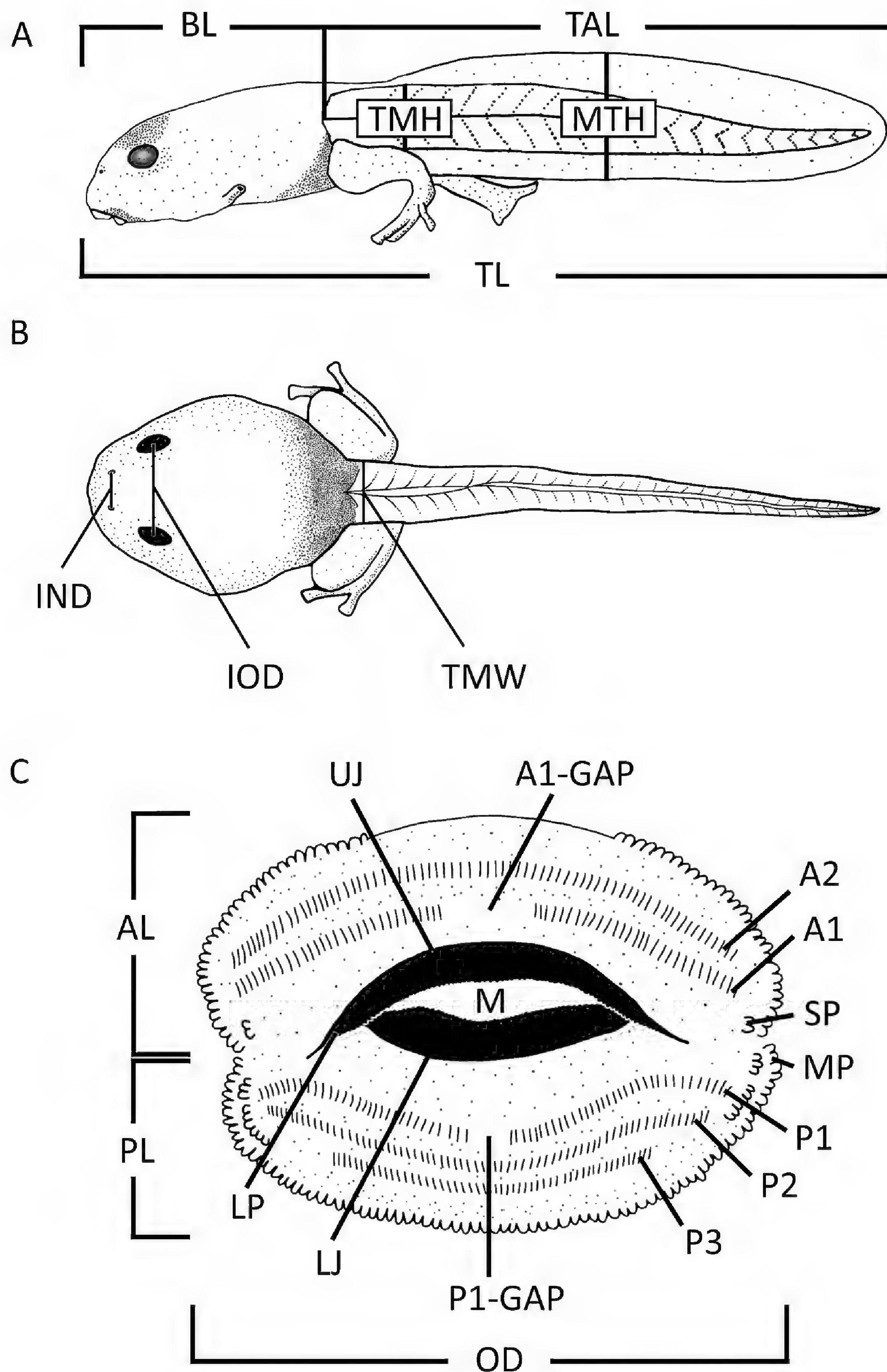


Fig. 2. Landmarks and measurements of a tadpole body and definitions of the oral apparatus. **A.** Lateral view. **B.** Dorsal view. **C.** Oral apparatus. Abbreviations A–B: BL=body length; TAL=tail length; TL=total length; TMH=tail muscle height; MTH=maximum tail height; IND=internarial distance; IOD=interorbital distance; TMW=tail muscle width. The dotted line indicates the accurate progression of the measurement which represents the body length. Abbreviations C: A1=first anterior tooth row; A2=second anterior tooth row; A2-GAP=medial gap in second anterior tooth row; AL=anterior (upper) labium; LJ=lower jaw sheath; LP=lateral process of upper jaw sheath; M=mouth; MP=marginal papillae; OD=oral disc; PL=posterior (lower) labium; P1=first posterior tooth row; P2=second posterior tooth row; P3=third posterior tooth row; SM=submarginal papillae; UJ=upper jaw sheath.

Table 1. *Ranitomeya amazonica* (n=5) larvae morphometric measurements at the stages 26–41. Not all stages are represented; all measurements are given in [mm]. Abbreviations: BL=body length; BWE=body width at eye level; BWN=body width at nostril level; ED=horizontal eye diameter; END=eye nostril distance; INFD=internarial distance; IOD=interorbital distance; MBH=maximum body height; MBW=maximum body width; MTH=maximum tail height; ODW=oral disc width; TAL=tail length; TMH=tail muscle height at base; TMW=tail muscle width at base; TL=total length; RED=rosto-eye distance, from tip of snout to the center of the eye in lateral view; RND=rosto-nasal distance, from tip of snout to the center of the nostril in lateral view; RSD=rosto-spiracle distance.

Stage	26	31	34	38	41
BL	5.15	7.12	8.33	8.33	9.38
BWE	3.79	4.24	4.70	5.00	5.57
BWN	2.73	2.73	3.03	3.33	3.14
ED	0.45	0.61	0.76	0.83	1.13
END	0.91	1.21	1.52	1.52	1.23
IND	1.14	1.36	1.52	1.59	1.57
IOD	1.97	2.42	2.73	3.08	3.00
MBH	2.05	3.03	3.18	3.18	4.14
MBW	3.94	5.15	5.76	5.91	7.00
MTH	1.97	3.00	3.33	3.03	3.71
ODW	1.14	1.79	1.97	1.97	1.86
TAL	10.30	13.79	15.15	15.15	18.29
TMH	0.91	1.67	1.82	1.74	2.14
TMW	1.06	1.67	1.97	2.12	2.29
TL	15.45	20.91	23.48	23.48	27.67
RED	1.52	1.97	2.42	2.42	2.15
RND	0.61	0.76	0.98	0.98	0.92
RSD	3.26	4.85	5.68	5.76	6.00
MBW/BL	0.76	0.72	0.69	0.71	0.75
RED/BL	0.29	0.28	0.29	0.29	0.23
ED/BL	0.09	0.09	0.09	0.10	0.12
RND/RED	0.40	0.38	0.41	0.41	0.43
IND/IOD	0.58	0.56	0.56	0.52	0.52
TMW/MBW	0.27	0.32	0.34	0.36	0.33
MBH/MBW	0.52	0.59	0.55	0.54	0.59
TAL/BL	2.00	1.94	1.82	1.82	1.95
TAL/TL	0.67	0.66	0.65	0.65	0.66
TMH/MTH	0.46	0.56	0.55	0.58	0.58
TMW/MBW	0.27	0.32	0.34	0.36	0.33
ODW/MBW	0.29	0.35	0.34	0.33	0.27
RSD/BL	0.63	0.68	0.68	0.69	0.64
BWN/BWE	0.72	0.64	0.65	0.67	0.56

rounded and transparent papillae are present at the posterior side, with a moderate medial gap, and absent at the anterior side, except the most lateral part (seven papillae). Submarginal papillae are absent. Anterior labium contains two tooth rows of the same width (A1, A2), large medial gap in second anterior tooth row (A2-GAP). Posterior labium contains three tooth rows (P1, P2, P3),

moderate medial gap in first tooth row (P1-GAP). Black jaw sheaths, both with serrations. The upper jaw sheath is wider than the lower jaw sheath. The labial tooth row formula is 2(2)/3(1) (Fig. 3D). Characteristic traits and the correlated proportions do not change during the development stages 26 to 41 (Table 1).

Table 2. *Ranitomeya amazonica* (n=4): development stages of embryos and hatchlings.

n=4	Day	Stage	Traits
Embryos	1	8	egg diameter 1.5 mm; eggs anthracite to dark gray; swam beneath the water surface; transparent egg integument; highly glutinous; no pigmentation
	2	10	eggs with brown pigmentation; dorsal lip visible
	3	13	neural plate visible
	4	–	
	5	19	large yolk sack present; embryonic body assumes larval shape; head and tail region visible; larva dun, spotted beige; gill buds present; mouth slightly perceptible
Hatchlings	6	20	elongation of the tail; gills present, circulation recognizable; tail fins slightly visible; myosepta visible; vent tube bud visible
	7	21–22	elongation of the tail and the gills; tail pointed; overall body size increased; upper and lower tail fins more transparent; denser pigmentation of body and tail region
	8	22	eyes visible; nares discernible; atrophy of the yolk sack initiated
	9	23–24	reduction of the right gill; oral apparatus discernible; yolk sack almost fully atrophied
	10	24–25	gills absent in 75% of the clutch; yolk sack completely atrophied
	11–12	25	gills absent; spiracle forming on the left

Coloration of a living tadpole of *R. amazonica* (ZFMK 97374). The dorsum is black to grey, with a yellowish green median stripe and two dorsolateral stripes of the same color, which run parallel to the longitudinal axis, and two lateral stripes (Fig. 3A1, A2). The two dorsolateral stripes originate at one point posterior to the nares, become separated and run next to the eyes to the base of the tail, with a moderate gap on eye level. The median one lies in between the two others, starts at eye level and ends prior to the tail-body junction. The lateral stripes are situated differently. One of the lateral stripes is situated at the first half of the body below the longitudinal axis, while the other one is located above the longitudinal axis at the second half of the body. The hindlimbs are dark bluish with large black spots. The tail shows a brownish coloration and is covered with dark and bright spots, the second half is brighter than the first half. Fins are transparent and spotted with beige dots. The density of dots wanes till the tip.

During metamorphosis, the dorsal coloration of tadpoles changed in regard to the different development stages (Fig. 4). Reaching stage 25 some specimens displayed a few isolated yellowish green spots while the majority showed no coloration. At stage 28 some parts of the medial and dorsolateral stripes were present at the first half of the dorsum. In comparison to the final coloration, those areas were yellowish green instead of yellow and lacked a continuous connection. At stage 36 the color pattern was yellow, the dorsolateral stripes reached the second half of the body and the medial stripe ended close to the posterior margin of the eyes. While the dorsolateral stripes were continuous, the medial stripe was spotted. At stage 41, the dorsolateral stripes reached the tail-body

junction and the medial line ended at the second half of the body. Moreover, each flank displayed the initiation of the ventrolateral stripes posterior to the forelimb pouches, which were visible in dorsal view, as well as the typical color pattern of the hindlimbs (Fig. 3C1, C2).

Coloration of a preserved tadpole of *R. amazonica* (ZFMK 97374). The dorsum is dark gray, with a brownish area at the forelimb pouches. Dorsolateral and median stripes are whitish and run on top or parallel to the longitudinal axis, clearly discernible on the head and the first half of the body. Dorsolateral stripes originate and bifurcate at one point posterior to the nares and run next to the eyes, with a moderate gap on eye level. The median stripe runs in between the eyes, not fusing with the origin of the dorsolateral stripes. The hindlimbs are bluish gray, spotted with dark dots. The tail is brownish; the first half is darker than the second one, which is almost transparent. Fins are transparent and spotted with beige dots. Ventral side has a dark grey to brown coloration, except one bright spot at the chin, posterior to the oral disc.

Larval staging. During their embryonic development, all four to six eggs of the same clutch develop at the same pace, except the reduction of the gills. While the majority of the eggs swam separately beneath the water surface, two in each clutch stayed as a pair (Fig. 5B). Eggs up to stage 10 were not pigmented (Fig. 5A). At stage 10, when the dorsal lip was visible, the pigmentation started and the eggs became brownish. After three days, the neural plate was discernible (Fig. 5C). Reaching stage 18, a whitish yolk sack was present at the ventral side of the embryo and body parts were slightly differentiat-

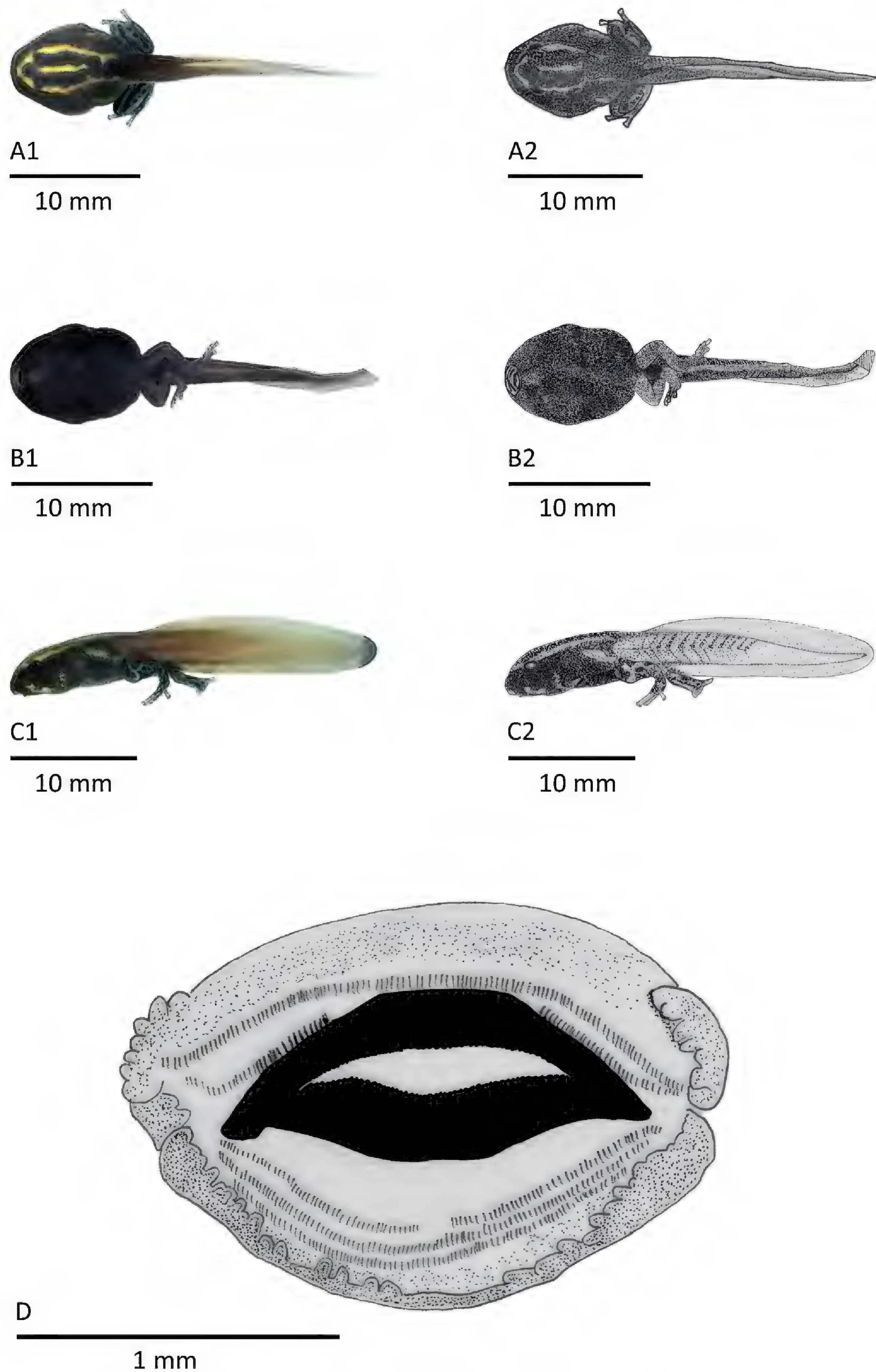


Fig. 3. Illustrations of the tadpole of *Ranitomeya amazonica*, stage 41 of Gosner (1960). **A1.** Dorsal view, photograph. **A2.** Dorsal view drawing. **B1.** Ventral view, photograph. **B2.** Ventral view, drawing. **C1.** Lateral view, photograph. **C2.** Lateral view, drawing. **D.** Drawing of the oral disc. LTRF=2(2)/3(1).



Fig. 4. Development of the color pattern of *Ranitomeya amazonica*. **A.** Tadpole at stage 25 with isolated colored spots. **B.** Tadpole at stage 25 without isolated colored spots. **C–D.** Different densities at Gosner stage 30. **E.** Tadpole at Gosner stage 36. **F.** Tadpole at Gosner stage 41, typical color pattern on hindlimbs.

ed (Fig. 5D). At stage 19, the embryo slowly assumed a larval shape. The head and tail region were visible and the larva had a dun coloration with beige spots. While the gill buds, the opening of the mouth and the ventral tube emerged, the eyes were absent. At stage 20, the gills and the correlated circulation were present while the whole body was elongated (Fig. 5E, Table 2). Upper and lower tail fins were slightly visible and the myosepta were present. Between stages 21 and 22, the tail and the gills were even more elongated, the overall body size increased and the pigmentation of all structures was denser. Tail fins were transparent, the tail was pointed. At stage 22, eyes were visible, nares were discernible and the decrease of the yolk sack was initiated (Fig. 5F). During the transition from stage 23 to 24, the sinistral gills were present while the dextral gills were completely reduced (Fig. 5G). The yolk sack was almost fully atrophied and the oral apparatus was formed. The transition to a free living and mobile tadpole started at stage 25, while the majority of the clutch was no longer enclosed by the jelly layer and the yolk sack was fully reduced. The spiracle was formed on the left, and after eleven to twelve days of development, the hatchlings swam freely within the water column (Fig. 5H–I).

Right after hatching, the free-swimming larvae had a surface area of $0.10 \pm 0.02 \text{ cm}^2$ (Table 3). Between the stages 25 to 27, while the hindlimb bud was slightly developed, the surface increased by 330%, resulting in an area of $0.33 \pm 0.20 \text{ cm}^2$. At stage 28, which half of the tadpoles had reached after 49 to 67 days (median=56 days), they had a mean surface area of $0.74 \pm 0.12 \text{ cm}^2$ (Table 3). The hindlimb bud was as long as wide and the dorsal color pattern was slightly visible at the first half of the body. Between stages 29 to 40, where the completion of the hindlimb development took place, the larvae had a mean surface area of $0.98 \pm 0.19 \text{ cm}^2$. Thus, all toes, the metatarsal tubercles and the subarticular patches were discernible. With an area of $1.17 \pm 0.12 \text{ cm}^2$, half of all tadpoles reached stage 41 after 69 to 88 days (median=84 days). Forelimb buds were visible and the hindlimbs showed the typical color pattern of the adult frog (Fig. 3A1, B1). Furthermore, colored dorsolateral stripes were discernible and the ventral tube as well as the oral apparatus was still present. While the forelimbs grew inside the body, during the transition from stage 41 to 42, the larvae reached their maximum size with a surface area of $1.19 \pm 0.12 \text{ cm}^2$. After 82 to 94 days (median=89 days), 50% of all metamorphs had emerged

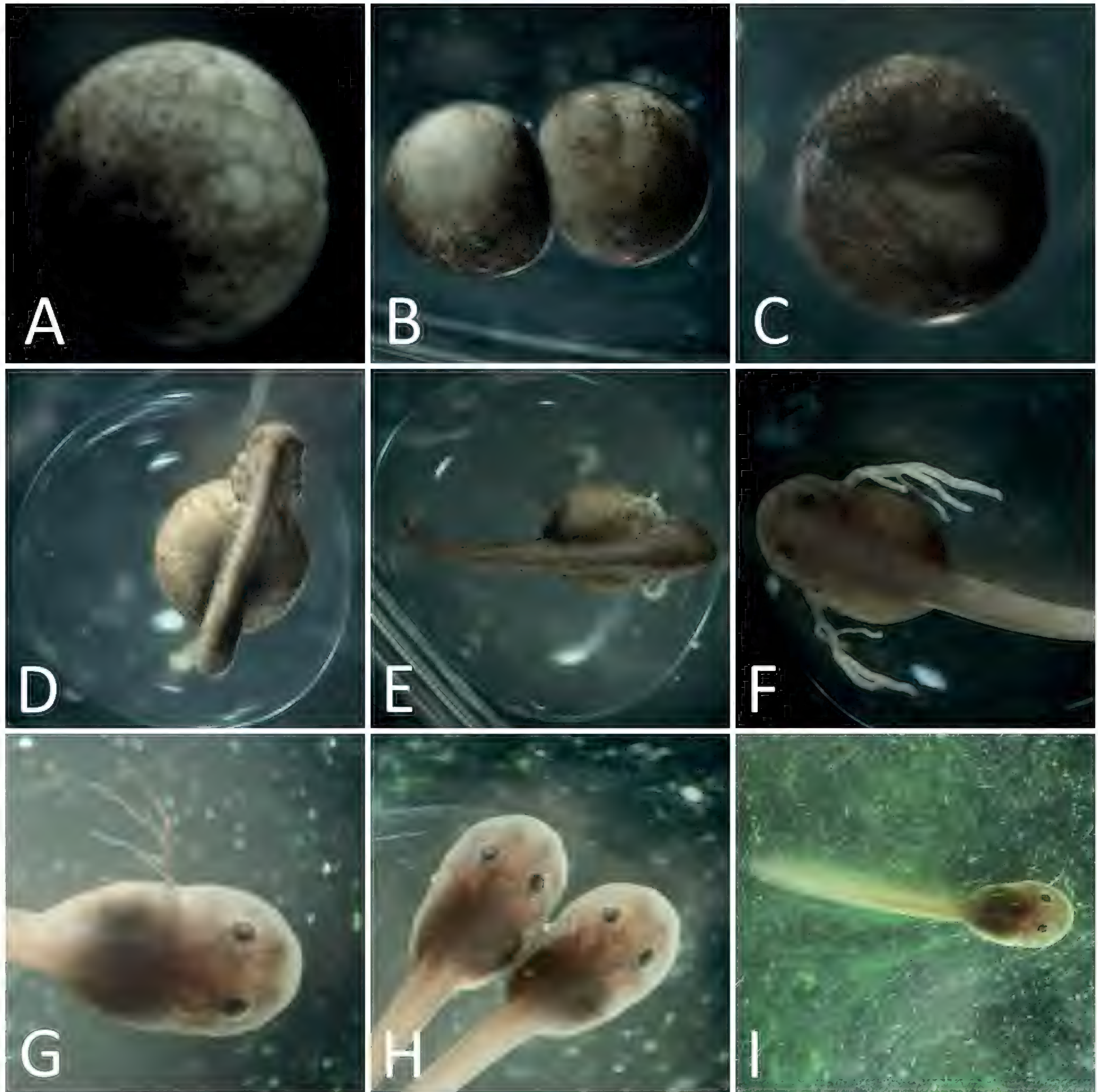


Fig. 5. Embryos and hatchlings of *Ranitomeya amazonica*. **A.** Isolated egg at stage 8. **B.** Egg pair at stage 9–12. **C.** Embryo at stage 13–14. **D.** Embryo at stage 18–19. **E.** Hatchling at stage 20. **F.** Hatchlings at stage 22. **G.** Hatchling at stage 23–24. **H.** Hatchlings at stage 25. **I.** Free swimming larva at stage 25–26.

forelimbs, while the surface area decreased to $1.08 \pm 0.17 \text{ cm}^2$. The resorption of the tail started after 91 to 99 days (median=96 days), while the tadpoles had a mean surface area of $0.86 \pm 0.15 \text{ cm}^2$. During the next days, the tail atrophied until the larva completed the metamorphosis, whereby the area of the larva was reduced to $0.82 \pm 0.15 \text{ cm}^2$. Thus, the transition from a free-swimming larva to a froglet with a remnant of the tail lasted 91 to 99 days (median=96 days), while some individuals needed less (84 days) and others more time (105 days, Fig. 6).

An additional and more detailed staging table, based on stereomicroscopic determinations of 17 specimens between stages 25 to 41, can be found in the Table 4.

The complete development, from the embryogenesis through hatching and larval period to metamorphosis, was observed under constant conditions with a temperature of 24°C while the annual mean temperature within the natural distribution area of *R. amazonica* is slightly higher ($T_{\text{Mean}} = 25.2^\circ\text{C}$, $T_{\text{Max}} = 28.5^\circ\text{C}$, $T_{\text{Min}} = 21.8^\circ\text{C}$; Karger et al. 2017a,b; Fig.7)

Table 3. *Ranitomeya amazonica* (n= 16) larvae and metamorphs development stages based on image analyses. Area [cm²] is highly correlated with body mass.

n=16	Stage (n)	Traits	Area [cm²]
Larvae	25 (16)	spiracle present; oral apparatus clearly visible; typical dorsal color pattern absent	0.10 ± 0.02
	25–27 (16)	hindlimb bud slightly developed, diameter < length; typical dorsal color pattern slightly visible at the first half of the body	0.33 ± 0.20
	28 (14)	length of the hindlimb bud equal to the diameter, no pigmentation	0.74 ± 0.12
	28–40 (14)	hindlimb bud length > diameter; foot paddle slightly visible; indentation between toes 4–5 and 3–4; indentation between toes 4–5, 3–4 and 2–3; Indentation between toes 4–5, 3–4, 2–3 and 1–2; toes 3–5 separated; all toes separated; metatarsal tubercle present; subarticular patches present; hindlimbs with pigmentation; typical dorsal color pattern present	0.98 ± 0.19
	41 (14)	forelimb buds present; typical color pattern on hindlimbs present; lateral stripes present	1.17 ± 0.12
Metamorphs	41–42 (14)	enlargement of the forelimb buds	1.19 ± 0.12
	42 (9)	forelimbs emerged	1.08 ± 0.17
	43 (10)	initiation of tail resorption	0.86 ± 0.15
	43–46 (10)	reduction of the tail until metamorphosis was completed	0.82 ± 0.15

Table 4. *Ranitomeya amazonica* (n=17) larval development stages based on stereomicroscopic determinations. Area [cm²] is highly correlated with body mass.

n=17	Stage (n)	Traits	Area [cm²]
Larvae	25 (3)	spiracle present; oral apparatus clearly visible; typical dorsal color pattern is absent	0.25 ± 0.01
	28 (5)	hind limb bud slightly developed, diameter ≤ length; typical dorsal color pattern slightly visible at the first half of the body	0.49 ± 0.09
	29 (9)	length of the hind limb bud 1.5 times of the diameter	0.59 ± 0.08
	30 (4)	length of the hind limb bud two times of the diameter	0.66 ± 0.07
	31 (4)	foot paddle is slightly visible, slight pigmentation at the base of the hind limb	0.75 ± 0.11
	33 (7)	indentation between toes 4–5 and 3–4	0.80 ± 0.14
	35 (9)	indentation between toes 4–5, 3–4, 2–3 and 1–2	0.87 ± 0.14
	36 (3)	toes 3–5 are separated; dorsal color pattern is denser and exceeds the first half of the body	1.28 ± 0.11
	39 (4)	all toes are separated; metatarsal tubercle is present; subarticular patches are present	1.30 ± 0.08
	41 (2)	forelimb buds are present; typical color pattern on hind limbs present; lateral stripes are present	1.36 ± 0.12

Ranitomeya benedicta Brown, Twomey, Pepper & Sanchez-Rodriguez, 2008

Breeding behavior in captivity. The breeding pair among the three available specimens mainly deposited their clutches of two to three eggs inside a dry and horizontally orientated film container which was attached to the cork tile. In rare cases, they placed the clutches within

the bromeliad phytotelm. Reproduction did not obey a standardized way.

Larval morphology. Tadpole description is based on one individual at stage 41 (ZFMK 97363). Further voucher specimens are ZFMK 97367 and 97376. According to McDiarmid & Altig (1999), the larva belongs to the exotrophic, lentic, benthic and arboreal larval type. All measurements that were used to calculate the following

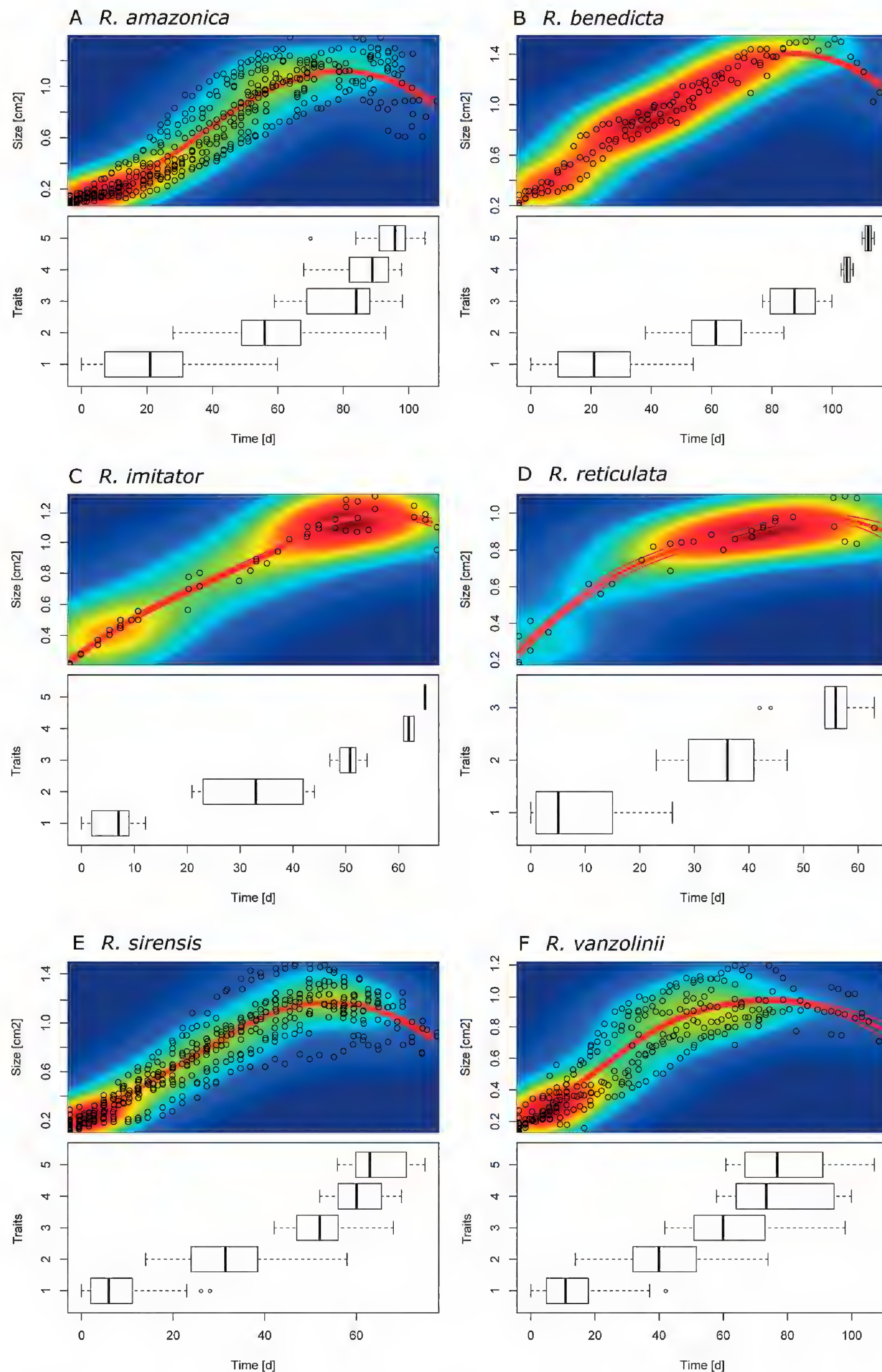


Fig. 6. Developmental series of six *Ranitomeya* species during the transition from a hatchling to a froglet. The upper panel illustrates the increase of surface area over time, whereby the surface area [cm²] is highly correlated with the body mass. Warmer colors indicate a higher sample density; each circle represents one data point. Loess function represented by the red lines, whereby the outer lines display the 95% confidence interval. The lower panel illustrates the temporal occurrence of the following traits: 1 = no limb bud discernible; 2 = hindlimb bud discernible; 3 = forelimb pouches discernible; 4 = forelimbs emerged; 5 = initiation of tail resorption.

proportions and its comparison with the other species of this study, are to be found in Appendix III.

Dorsal view: The body is oval shaped and moderately elongated ($MBW/BL=0.78$). The snout is short and rounded ($RED/BL=0.18$, $BWN/BWE=0.57$). The nares are positioned and orientated laterally; their shape is not visible in dorsal view. A skin fold connects the nares with the anterior edge of the eyes. Nares are closer to the snout than to the eyes ($RND/RED=0.41$). The eyes are large ($ED/BL=0.11$), positioned dorsally and orientated laterally. Internarial distance is smaller than the interorbital distance ($IND/IOD=0.40$). The single and sinistral spiracle is not visible in dorsal view.

Lateral view: The body is depressed ($MBH/MBW=0.59$), the snout pointed. Nares are small and elliptical. The spiracle is situated below the longitudinal axis, at the second half of the body ($RSD/BL=0.56$). The inner wall of the spiracle is free from the body, the opening is round, and the spiracle tube is short. Maximum body height is situated posterior to the eye. The tail is long and rounded ($TAL/BL=2.06$, $TAL/TL=0.67$), the musculature well developed ($TMH/MTH=0.62$, $TMW/MBW=0.33$). The “V”-shaped myosepta are visible along the whole length of the tail. Both tail fins are of the same height and originate posterior to the tail-body junction, the lower fin slightly anterior to the upper fin. The ventral tube is small, dextral; emergence from abdomen is sagittal, opening is elliptical. Hindlimbs are fully developed. Oral apparatus is visible in lateral view.

Oral apparatus: The oral disc is elliptical, positioned ventrally and covers nearly one third of the body width ($ODW/MBW=0.29$), emarginated. Marginal, ensiform, rounded and transparent papillae are present at the posterior labium and absent at the anterior labium, except

the most lateral part (five papillae). Submarginal papillae are absent. The anterior labium contains two tooth rows (A1, A2) of the same width, whereas the second row is divided by a large medial gap (A2-GAP). The posterior labium contains three rows of teeth (P1, P2, P3) with a moderate medial gap in the first tooth row (P1-GAP). P1 P2 and P3 have the same width. Both jaw sheaths are black and serrated. The upper jaw sheath is wider than the lower jaw sheath. Lateral processes are present, extending barely past the lower jaw. The tooth row formula is 2(2)/3(1) (Fig. 8D).

Coloration of a living tadpole of *R. benedicta* (ZFMK 97363). The basic color of the dorsum is black to dark gray, with a reddish area anterior and posterior to the eyes, which starts posterior to the nares and ends at the first half of the body in dorsal view (Fig. 8A1, A2). In between both eyes light coloration is lacking, except one narrow stripe which connects the posterior and anterior part of the color pattern. The hindlimbs are as black as the dorsum. The tail is brownish beige and covered with darker dots. Fins are transparent and spotted with beige dots.

Coloration of a preserved tadpole of *R. benedicta* (ZFMK 97363). The basic color of the dorsum is dark gray, except some brighter areas at the forelimb pouches and at the muscle attachment of the tail. Additionally, there is a bright area anterior and posterior to the eyes. While the anterior part is bright orange, the posterior part is auburn. Both parts are fused medially, creating a face mask. The hindlimbs are as gray as the dorsum, with some slightly bright areas at the tip of the toes. The tail is beige, covered with grayish dots; the first half is brighter

Table 5. *Ranitomeya benedicta* (n=4) larvae and metamorphs development stages based on image analyses. Area [cm²] is highly correlated with body mass.

n=4	Stage (n)	Traits	Area [cm²]
Larvae	25(4)	sinistral spiracle present; oral apparatus clearly visible	0.23 ± 0.04
	25–27(4)	hindlimb bud slightly visible, length < diameter; body depressed	0.60 ± 0.24
	28 (3)	length of the hindlimb bud equal to the diameter, no pigmentation	1.01 ± 0.11
	28–40 (3)	hindlimb bud length > diameter; foot paddle slightly visible; indentation between toes 4–5 and 3–4; indentation between toes 4–5, 3–4 and 2–3;	1.20 ± 0.16
		Indentation between toes 4–5, 3–4, 2–3 and 1–2; toes 3–5 separated; all toes separated; metatarsal tubercle present; subarticular patches present; hindlimbs with pigmentation; typical dorsal color pattern present	
Metamorphs	41 (3)	forelimb buds present; typical color pattern on hindlimbs present	1.38 ± 0.13
	41–42 (3)	enlargement of the forelimb buds	1.45 ± 0.09
	42 (1)	forelimbs emerged	1.39
	43 (1)	initiation of tail resorption	1.03 ± 0.00
	43–46 (1)	reduction of the tail until metamorphosis was completed	1.00 ± 0.13

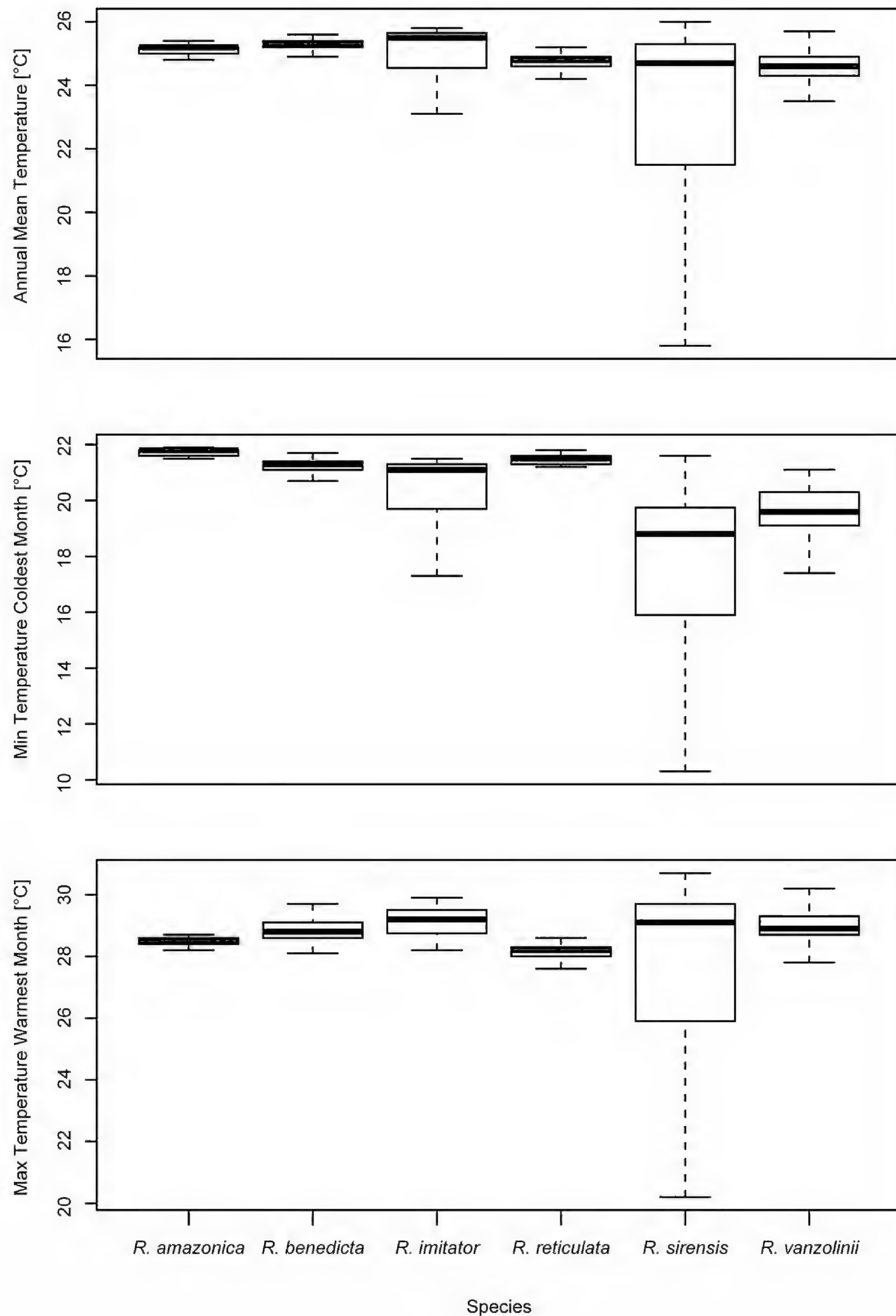


Fig. 7. Climatic characteristics within the geographic ranges of six *Ranitomeya* species in terms of annual mean temperature, minimum and maximum temperature of the coldest / warmest month. Boxplots show the 95% range, lower and upper hinge enclosing 50% of the samples and the median based on a random sample per 10 km².

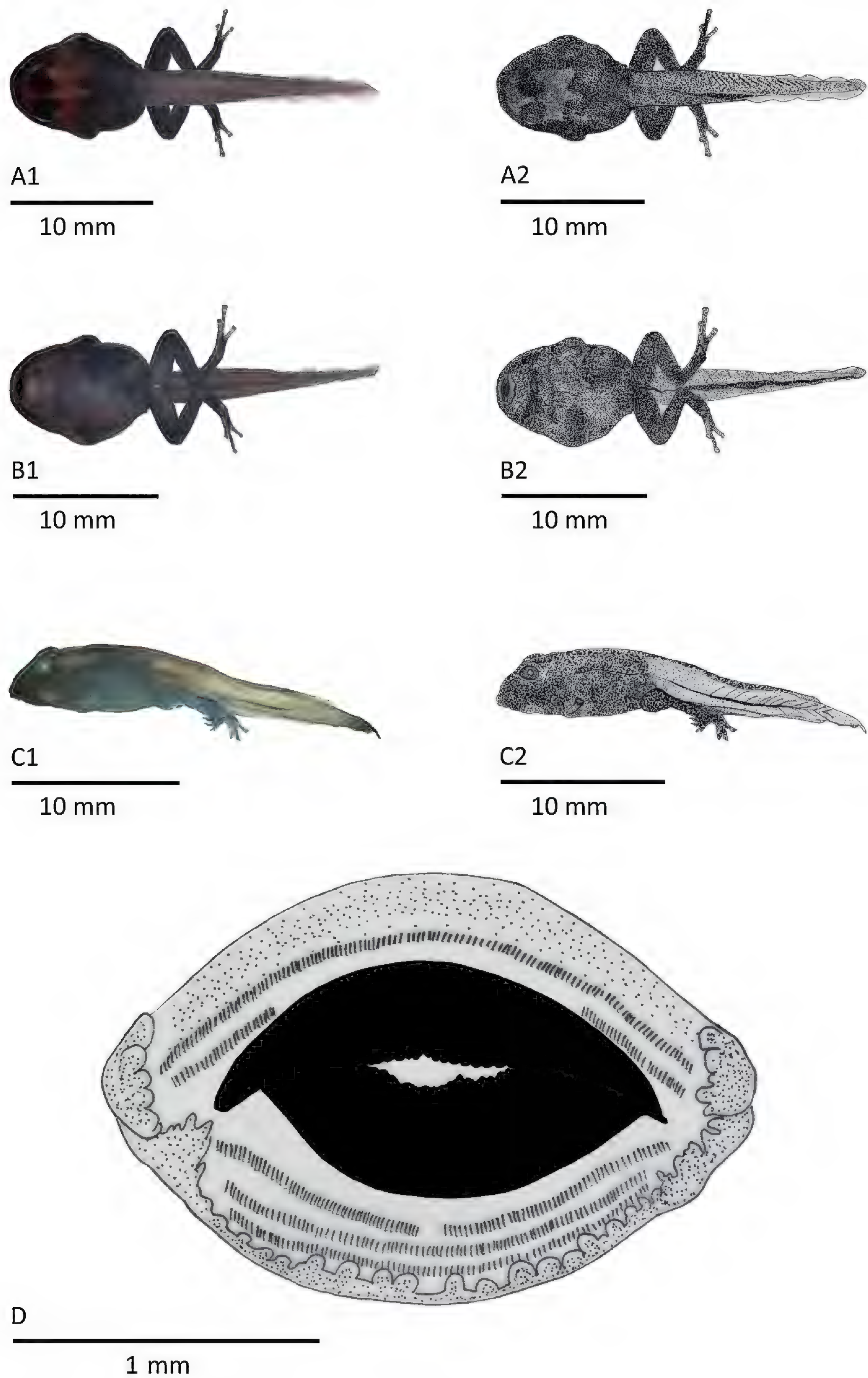


Fig. 8. Illustrations of the tadpole of *Ranitomeya benedicta*, stage 41 of Gosner (1960). **A1.** Dorsal view, photograph. **A2.** Dorsal view, drawing. **B1.** Ventral view, photograph. **B2.** Ventral view, drawing. **C1.** Lateral view, photograph. **C2.** Lateral view, drawing. **D.** Drawing of the oral disc. LTRF = 2(2)/3(1).

than the second half. The ventral side is as gray as the dorsum, with an auburn area around the oral disc which fades till the tail-body junction.

Larval staging. Right after hatching, the free-swimming larvae had a surface area of $0.23 \pm 0.04 \text{ cm}^2$ (Table 5). During the transition from stage 25 to 27, while the hindlimb buds were slightly visible, the surface area increased to $0.60 \pm 0.24 \text{ cm}^2$ (Table 5). This development period lasted for at least 54 to 70 days (median=61 days), when half of all individuals reached stage 28. At this point the hindlimb buds were equal in length and diameter and therefore clearly discernible, while the tadpoles had reached a surface area of $1.01 \pm 0.11 \text{ cm}^2$. Between stages 29 to 40, where the completion of the hindlimb development took place, the tadpoles had a mean surface area of $1.20 \pm 0.16 \text{ cm}^2$. Thus, all toes, the metatarsal tubercles as well as the subarticular patches were discernible. After 80 to 94 days (median=88 days), 50% of the individuals reached stage 41. The forelimb pouches were visible and the larvae had a surface area of $1.38 \pm 0.13 \text{ cm}^2$. While the forelimbs evolved within the body, during the transition from stage 41 to 42, the tadpoles reached the peak of their growth with an area of $1.45 \pm 0.09 \text{ cm}^2$. After 105 days, the forelimbs emerged and the remaining larva reached stage 42. Seven days later, the resorption of the tail was initiated, ensuring the transition from a hatchling to a young froglet. Therefore, the area of the metamorph was reduced to a size of $1.00 \pm 0.13 \text{ cm}^2$. Altogether, the development from a free-swimming larva to a young froglet lasted around 114 days (Fig. 6).

The development was observed under constant conditions with a temperature of 24°C , while the annual mean temperature within the natural distribution area of *R. benedicta* is slightly higher ($T_{\text{Mean}} = 25.3^\circ\text{C}$, $T_{\text{Max}} = 28.8^\circ\text{C}$, $T_{\text{Min}} = 21.3^\circ\text{C}$; Karger et al. 2017a, b; Fig. 7).

Ranitomeya imitator (Schulte, 1986)

Breeding behavior in captivity. The single breeding pair deposited the clutches of one to two whitish to beige eggs directly in the bromeliad phytotelm or in a horizontally orientated film container, which was attached to the side wall of the terrarium, which was kept moist by the misting system. Reproduction did not obey a standardized way.

Larval morphology. Description of the tadpole is based on two specimens at stage 41 (ZFMK 97358). Further voucher specimens are ZFMK 97364, 97368 and 97377. According to McDiarmid & Altig (1999), the larvae belong to the exotrophic, lentic, benthic and arboreal larval type. All measurements that were used to calculate the following proportions and its comparison with the other species of this study, can be found in Appendix III.

Dorsal view: The body is shaped elliptically and slightly elongated ($\text{MBW}/\text{BL} = 0.75$). The snout is short, rounded and moderately pointed ($\text{RED}/\text{BL} = 0.26$, $\text{BWN}/\text{BWE} = 0.65$). The shape of the nares is not visible in dorsal view. A skin fold, which originates at the nares, ends close to the anterior margin of the eyes; the two landmarks are not connected. Nares are located closer to the snout than to the eyes ($\text{RND}/\text{RED} = 0.39$). Eyes are large ($\text{ED}/\text{BL} = 0.09$), situated dorsally and orientated laterally. Internarial distance is smaller than the interorbital distance ($\text{IND}/\text{IOD} = 0.46$). The single sinistral spiracle is not visible in dorsal view.

Lateral view: Body is depressed ($\text{MBH}/\text{MBW} = 0.73$), snout is pointed. Nares are round, positioned and orientated dorsally. The spiracle is positioned below the longitudinal axis, at the posterior part of the body ($\text{RSD}/\text{BL} = 0.56$), the inner wall is free from the body and the opening is round, spiracle tube is short. The maximum body height is situated between the eyes and the tail-body junction. The tail is long and the tip is broadly rounded ($\text{TAL}/\text{BL} = 1.83$, $\text{TAL}/\text{TL} = 0.65$). The musculature is well developed ($\text{TMH}/\text{MTH} = 0.49$; $\text{TMW}/\text{MBW} = 0.34$). The “V”- shaped myosepta are visible along the whole length of the tail, particularly in the first half. The upper fin originates anterior, the lower posterior to the tail-body junction. Upper fin is slightly higher than lower fin. Ventral tube partially absorbed, dextral; emergence from the abdomen sagittal, the opening is triangular and has smooth edges. Hindlimb development is completed. Parts of the oral apparatus are visible in lateral view, particularly the margins.

Oral apparatus: The oral disc is shaped elliptically, positioned ventrally, emarginated and covers almost one third of the body width ($\text{ODW}/\text{MBW} = 0.31$). Two rows of marginal, ensiform, rounded and transparent papillae are present at the posterior labium (around 20 papillae) and except one short row at the most lateral part, absent at the anterior labium (three to five papillae). Submarginal papillae are absent. The anterior labium contains two tooth rows of equal width (A1, A2) with a large medial gap in the second row (A2-GAP). The posterior labium contains three tooth rows (P1, P2, P3) with a moderate medial gap in the first tooth row (P1-GAP). Black jaw sheaths, both serrated. Upper jaw sheath is wider than the lower jaw sheath. Lateral processes are present, extending slightly past the lower jaw. Tooth row formula is 2(2)/3(1) (Fig. 9D).

Coloration of a living tadpole of *R. imitator* (ZFMK 97358). The basic color of the dorsum is beige, heavily covered with puce to black dots. Additionally, the first half of the body is strongly dotted with yellowish green spots, which are able to reflect the light and become golden yellow, while the second half is almost completely covered with black dots, except some single yellowish green spots. The hindlimbs are beige with dark spots. The

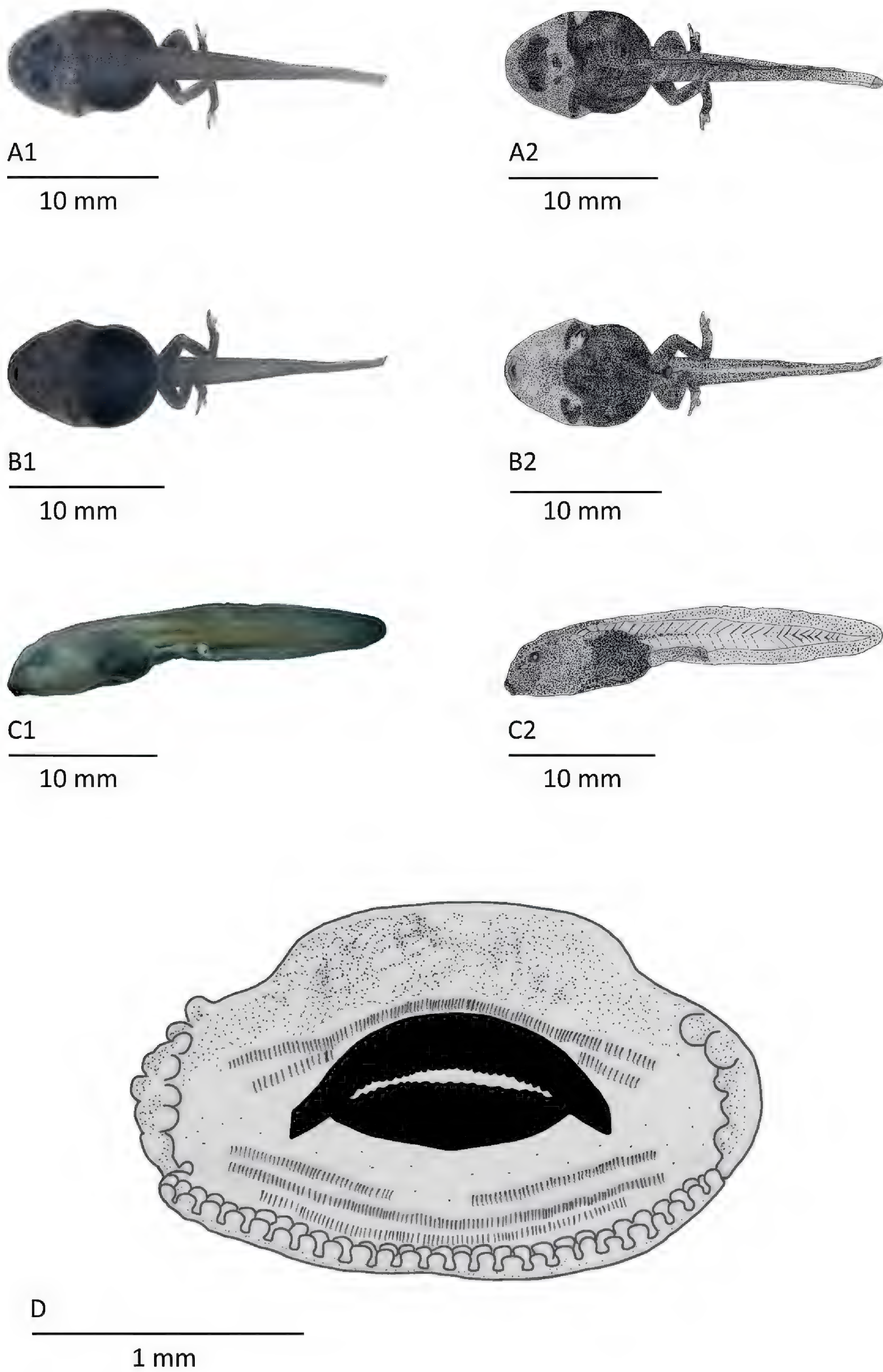


Fig. 9. Illustrations of the tadpole of *Ranitomeya imitator*, stage 41 of Gosner (1960). **A1.** Dorsal view, photograph. **A2.** Dorsal view, drawing. **B1.** Ventral view, photograph. **B2.** Ventral view, drawing. **C1.** Lateral view, photograph. **C1.** Lateral view, drawing. **D.** Drawing of the oral disc. LTRF = 2(2)/3(1).

tail is dun and spotted with puce dots; the second half is brighter than the first one. Fins are transparent and spotted with beige dots.

Coloration of a preserved tadpole of *R. imitator* (ZFMK 97358). Dorsum is beige, densely spotted with gray dots, with some brighter areas at the forelimb pouches and the muscle structures at the tail-body junction. The hindlimbs and the tail are of the same color as the dorsum, spotted with gray dots. While the dots on the hindlimbs are evenly distributed along their length, the

pigmentation of the tail decreases towards the tip. The fins are transparent and spotted with gray dots. The ventral side is beige and spotted with gray dots, while the concentration of that pigmentation increases to the tail-body junction.

Larval staging. One egg with a diameter of around 1.2 mm was found within a bromeliad phytotelm, where it swam beneath the water surface. At this time, it was not pigmented, had a transparent egg integument and was encompassed by a highly glutinous layer (Fig. 10A).

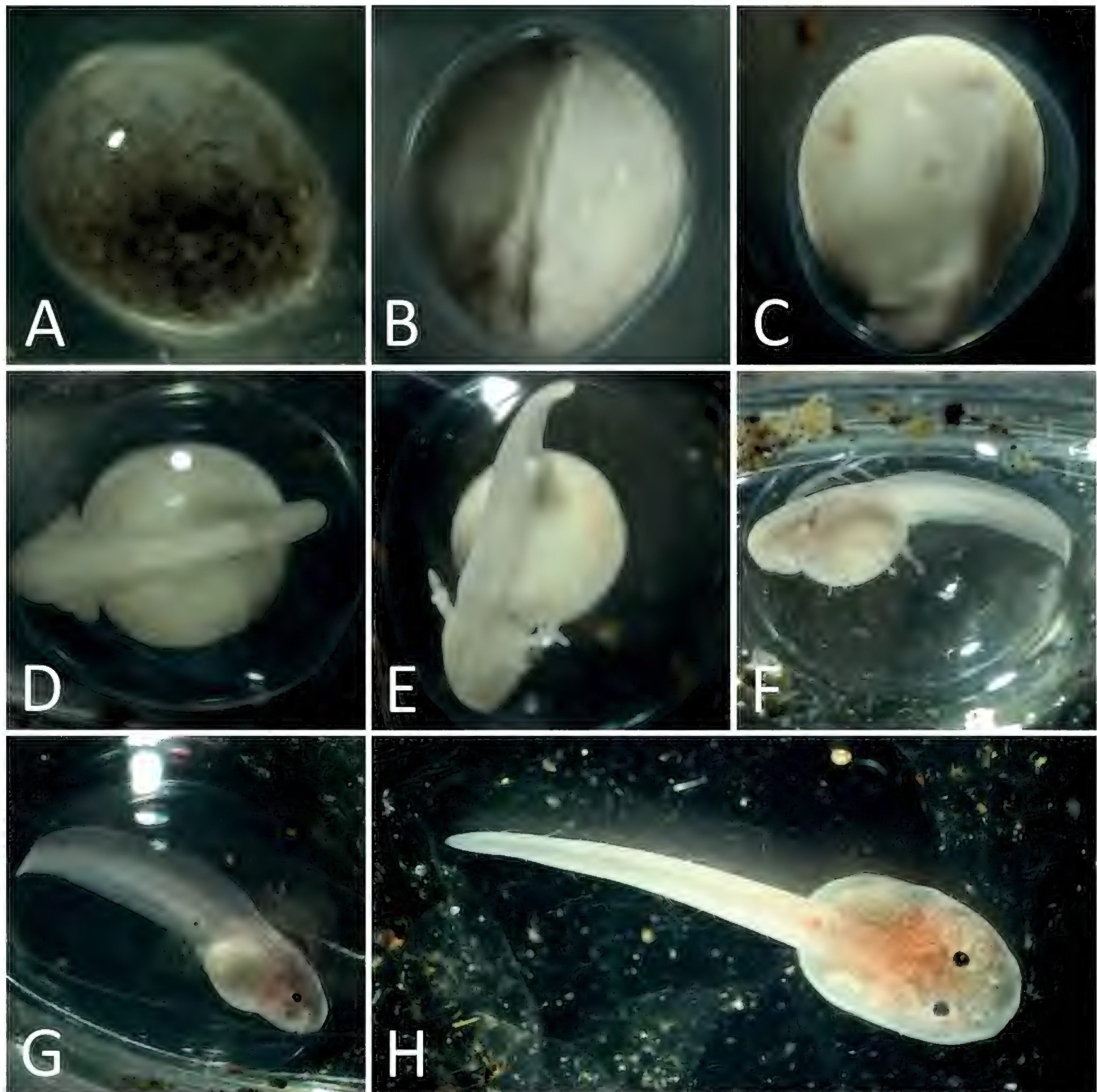


Fig. 10. Embryos and hatchlings of *Ranitomeya imitator*. **A.** Isolated egg at stage 8. **B.** Embryo at stage 14–15. **C.** Embryo at stage 16–17. **D.** Embryo at stage 19. **E.** Embryo at stage 20. **F.** Hatchling at stage 21. **G.** Hatchling at stage 24. **H.** Free swimming larva at stage 25–26. Picture C is from a different clutch.

Table 6. *Ranitomeya imitator* (n=1) embryo and hatchling development stages.

n=1	Day	Stage	Traits
Embryos	1	8	egg diameter 1.2 mm; egg whitish to beige; cells moderately large; swam beneath the water surface; transparent egg integument; highly glutinous; no pigmentation
	2	9	egg coloration paler than before; higher number of smaller cells
	3	11	yolk plug visible
	4	14	neural fold present
	5	19	large yolk sack present; embryonic body assumes larval shape; head and tail region visible; larva pale; gill buds present
Hatchlings	6	20	elongation of the tail; gills present; circulation recognizable; tail fins slightly visible; myosepta visible; vent tube bud visible
	7	21–22	elongation of the tail and the gills; tail pointed; overall body size increased; upper and lower tail fins more transparent; denser pigmentation of body and tail region
	8	22	elongation of the gills; eyes visible; atrophy of the yolk sack initiated
	9	22	tail fins are higher; pigmentation of the body denser; nares are discernible; yolk sack covered with blood vessels
	10	23	tail fins transparent and spotted with dots; yolk sack almost completely atrophied; oral apparatus discernible
	11–12	24	dextral gills absent, sinistral gills present; pigmentation of body and tail denser, spotted with beige dots; upper tail fin spotted with dark dots, lower tail fin with bright dots; anterior and posterior labia discernible; papillae present
	13	24	sinistral gill partially reduced; yolk sack completely atrophied; maximum body width in the second half of the body
	14–15	25	gills absent; spiracle forming on the left
	16	25	upper and lower jaw sheath visible (black); larva hatched

Table 7. *Ranitomeya imitator* (n=3) larvae and metamorphs development stages based on image analyses. Area [cm²] is highly correlated with body mass.

n=3	Stage (n)	Traits	Area [cm²]
Larvae	25 (3)	spiracle present; oral apparatus clearly visible; typical dorsal color pattern absent	0.22 ± 0.00
	25–27 (3)	hindlimb bud slightly developed, diameter < length; typical dorsal color pattern slightly visible at the first half of the body	0.39 ± 0.12
	28 (3)	length of the hindlimb bud equal to the diameter, no pigmentation	0.69 ± 0.11
	28–40 (3)	hindlimb bud length > diameter; foot paddle slightly visible; indentation between toes 4–5 and 3–4; indentation between toes 4–5, 3–4 and 2–3; Indentation between toes 4–5, 3–4, 2–3 and 1–2; toes 3–5 separated; all toes separated; metatarsal tubercle present; subarticular patches present; hindlimbs with pigmentation; typical dorsal color pattern present	0.89 ± 0.16
	41 (3)	forelimb buds present; typical color pattern on hindlimbs present	1.11 ± 0.04
Metamorphs	41–42 (2)	enlargement of the forelimb buds	1.18 ± 0.09
	42 (2)	forelimbs emerged	1.20 ± 0.17
	43(2)	initiation of tail resorption	1.03 ± 0.10
	43–46 (2)	reduction of the tail until metamorphosis was completed	1.03 ± 0.10

Table 8. *Ranitomeya imitator* (n=4) larval development stages based on stereomicroscopic determinations. Area [cm²] is highly correlated with body mass.

n=4	Stage (n)	Traits	Area [cm ²]
Larvae	25(1)	sinistral spiracle present; oral apparatus clearly visible; first half of the body brighter than the second half; first half of the tail darker than second half	0.20
	26 (1)	hindlimb bud slightly developed, length < ½ diameter	0.25
	28 (1)	length of the hindlimb bud equal to the diameter	0.40
	29 (1)	length of the hindlimb bud 1.5 times of the diameter	0.59
	30 (1)	length of the hindlimb bud two times of the diameter	0.69
	31 (1)	foot paddle slightly visible	0.75
	33 (1)	indentation between toes 4–5 and 3–4	0.82
	34(1)	indentation between toes 4–5, 3–4 and 2–3; dorsal color pattern slightly visible	1.02± 0.03
	35 (1)	indentation between toes 4–5, 3–4, 2–3 and 1–2; hindlimbs with pigmentation	1.09
	36 (2)	toes 3–5 separated	1.15 ± 0.09
	37 (2)	all toes separated; metatarsal tubercle present; subarticular patches present	1.16 ± 0.05
	41	forelimb buds present; typical color pattern on hind limbs present	1.18 ± 0.09

After one day it reached stage 9, the coloration became paler and the number of discernible cells increased (Table 6). At day three the egg reached stage 11 and the yolk plug was visible, followed by the neural fold at day four (Fig. 10B). A large yolk sack was discernible and the embryonic body assumed a larval shape at stage 19 (Fig. 10D). Thus, the head and tail region became visible and the gill buds were present. After six days of development the gills were discernible and the tail underwent several changes. The upper and lower tail fins together with the myosepta were slightly visible, while the whole tail was elongated (Fig. 10E). That elongation went on until day eight, as the hatchling reached stage 22.

The tail was pointed, the overall body size and the area of the gills increased, whereby the yolk sack atrophied. The pigmentation of the body and tail region became denser; the tail fins more transparent (Fig. 10F). At day nine, the hatchling was still at stage 22. The tail fins were higher, the nares discernible and the yolk sack was covered with blood vessels. When the larva reached stage 23, the transparent tail fins were spotted with beige dots, the oral apparatus was clearly visible and the yolk sack was almost completely atrophied. During day eleven and twelve, at stage 24, the dextral gill was reduced while the sinistral gill was still present (Fig. 10G). Additionally, the pigmentation of the body and tail region became denser and the anterior and posterior labia together with the papillae were discernible. At stage 25, both gills were absent while the sinistral spiracle was present. After 16 days of development the tadpole hatched from the jelly layer and swam free in the water body (Fig. 10H). At this time it had a surface area of 0.22 cm² (Table 7).

Between stages 25 to 27, where the hindlimb bud was slightly discernible, the larvae had a surface area of 0.39 ± 0.12 cm² (Table 7). After 24 to 43 days (median=34 days), half of all individuals had a hindlimb bud that was

equally in width and length and a surface area of 0.69 ± 0.11 cm² (Table 7). Between stages 28 to 40, the tadpoles had a surface area of 0.89 ± 0.16 cm². During this development period, the hindlimbs grew, all toes became separated and the typical dorsal color pattern was discernible. After 48 to 53 days (median=51 days), 50% of the tadpoles reached stage 41, with a surface area of 1.11 ± 0.04 cm². The forelimb buds were clearly perceptible and the hindlimbs displayed their typical reticulated color pattern. The forelimbs emerged after around 63 days, while the larvae reached their peak of growth with a surface area of 1.20 ± 0.17 cm², followed by the resorption of the tail after 67 days. During the transition to a young froglet, the surface area decreased to a mean value of 1.03 ± 0.10 cm² (Fig. 6, Table 7). A more detailed staging table based on stereomicroscopic determinations of four specimens between stages 25 to 37 can be found within Table 8.

The development was observed under constant conditions with a temperature of 24 °C, while the annual mean temperature within the natural distribution area of *R. imitator* is slightly higher ($T_{\text{Mean}} = 25.5$ °C, $T_{\text{Max}} = 29.2$ °C, $T_{\text{Min}} = 21.1$ °C; Karger et al. 2017a,b; Fig. 7).

Ranitomeya reticulata (Boulenger, 1884)

Breeding behavior in captivity. The breeding pair deposited the clutches, consisting of an egg, within the bromeliad phytotelm. Reproduction was occasionally.

Larval morphology. Description is based on three tadpoles at developmental stage 41 (ZFMK 97359). Further voucher specimens are ZFMK 97360, 97365 and 97378. According to McDiarmid & Altig (1999), the larvae belong to the exotrophic, lentic, benthic and arboreal larval type. All measurements that were used to calculate the

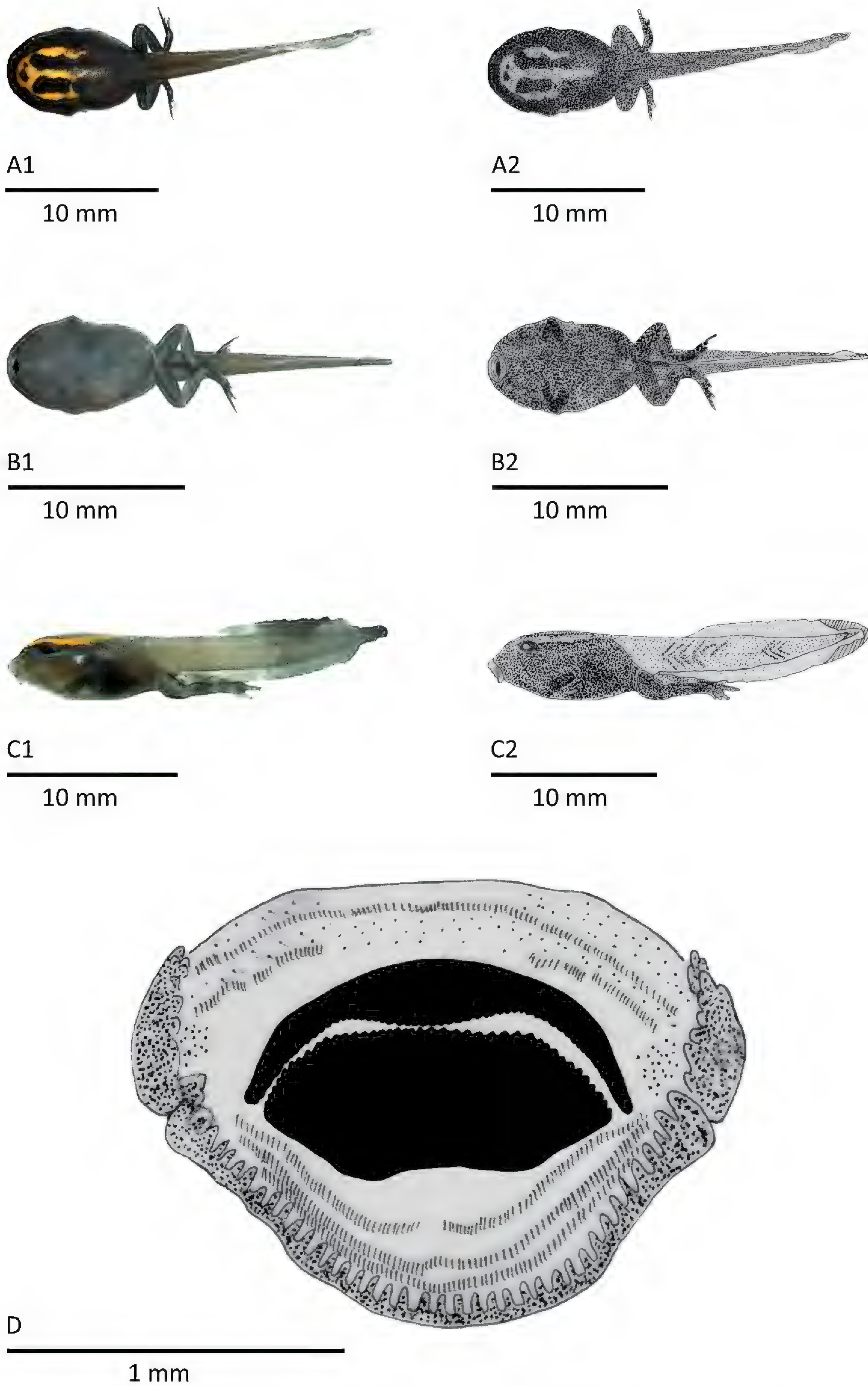


Fig. 11. Illustrations of the tadpole of *Ranitomeya reticulata*, satage 41 of Gosner (1960). **A1.** Dorsal view, photograph. **A2.** Dorsal view, drawing. **B1.** Ventral view, photograph. **B2.** Ventral view, drawing. **C1.** Lateral view, photograph. **C2.** Lateral view, drawing. **D.** Drawing of the oral disc. LTRF = 2(2)/3(1).

Table 9. *Ranitomeya reticulata* (n=3) larvae development stages based on image analyses. Area [cm²] is highly correlated with body mass. Note that data concerning metamorphs is missing as no specimen reached this stage.

n=3	Stage (n)	Traits	Area [cm ²]
Larvae	25 (3)	spiracle present; oral apparatus clearly visible; typical dorsal color pattern absent	0.23 ± 0.09
	25–27 (3)	hindlimb bud slightly developed, diameter < length	0.32 ± 0.11
	28 (2)	length of the hindlimb bud equal to the diameter, no pigmentation	0.81 ± 0.01
	28–40 (2)	hindlimb bud length > diameter; foot paddle slightly visible; indentation between toes 4–5 and 3–4; indentation between toes 4–5, 3–4 and 2–3; Indentation between toes 4–5, 3–4, 2–3 and 1–2; toes 3–5 separated; all toes separated; metatarsal tubercle present; subarticular patches present; hindlimbs with pigmentation; typical dorsal color pattern discernible	0.88 ± 0.06
	41 (2)	forelimb buds present; typical color pattern on hindlimbs present	1.02 ± 0.11

Table 10. *Ranitomeya reticulata* (n=5) larval development stages based on stereomicroscopic determinations. Area [cm²] is highly correlated with body mass.

n=5	Stage (n)	Traits	Area [cm ²]
Larvae	31 (3)	foot paddle is present; hindlimb bud length is two times of the diameter	0.53 ± 0.01
	34 (2)	indentation between toes 4–5, 3–4 and 2–3	0.64 ± 0.13
	36 (5)	indentation between toes 4–5, 3–4, 2–3 and 1–2; toes 3–5 are separated; dorsal color pattern extends from the posterior edge of the nares to the second half of the body	0.72 ± 0.08
	37 (4)	all toes are separated	0.77 ± 0.06
	39 (5)	subarticular patches present; dorsal color pattern is denser, has cross connections and ends at tail-body junction	0.80 ± 0.05
	41 (5)	forelimb buds are visible; vent tube is still present	0.78 ± 0.02

following proportions and its comparison with the other species of this study, are be found in the Table 13.

Dorsal view: The body is oval and elongated (MBW/BL=0.62). The snout is short and moderately pointed (RED/BL=0.28, BWN/BWE=0.65). The shape of the nares is not visible in dorsal view, nares are closer to the snout than to the eyes (RND/RED=0.40). A skin fold, which originates at the nares, ends close to the anterior margin of the eyes; the two landmarks are not connected. The eyes are large (ED/BL=0.09), positioned dorsally and orientated laterally. The internarial distance is smaller than the interorbital distance (IND/IOD=0.53). The single, sinistral spiracle as well as parts of the oral apparatus are visible in dorsal view.

Lateral view: Body is slightly depressed (MBH/MBW=0.68), the snout is pointed. Nares are round, located and orientated dorsally. The spiracle is situated below the longitudinal axis, at the second half of the body (RSD/BL=0.64), the inner wall is free from the body and the opening is round. The maximum body height is located posterior to the eye. The tail is long and moderately pointed (TAL/BL= 1.64, TAL/TL=0.62). The “V”-shaped myosepta are visible along the whole length of the tail. The upper fin originates posterior to the lower

fin and the tail-body junction, the margin of the lower fin is nearly parallel to the margin of the tail muscle. Ventral tube is strongly atrophied, emergence from abdomen sagittal. Hindlimbs are completely developed. Oral apparatus is visible in lateral view.

Oral apparatus: The oral disc is elliptical, emarginated, located anteroventrally and covers more than one third of the maximum body width (ODW/MBW=0.40). Marginal, pointed and pigmented papillae are present at the posterior labium and except the most lateral part, absent at the anterior labium. Submarginal papillae are absent. The anterior labium contains two tooth rows of an equal width (A1, A2), the second tooth row has a large medial gap (A2-GAP). The posterior labium contains three tooth rows (P1, P2, P3), with a moderate gap in the first row (P1-GAP). Tooth row P1 and P2 are of the same width, the width of the P3 was not discernible. Both jaw sheaths are black and serrated. The tooth row formula is 2(2)/3(1) (Fig. 11D).

Coloration of a living tadpole of *R. reticulata* (ZFMK 97359). The dorsum has an anthracite basic color, with three golden to orange stripes running on top or parallel to the longitudinal axis (Fig. 11A1, A2). The two dorso-

lateral stripes originate at one point posterior to the nares, bifurcate and run close to the eyes, with a moderate gap on eye level. The medial stripe runs in between the two others, situated on the symmetry line of the body. Depending on the specimen, the medial and the dorsolateral stripes are fused, originating from one point posterior to the nares and anterior to the eyes. The distance between the stripes decreased at the second half of the body. The hindlimbs and the tail are as anthracite as the dorsum, spotted with darker dots. Fins are transparent and spotted with grayish dots.

Coloration of a preserved tadpole of *R. reticulata* (ZFMK 97359). The dorsum has a beige basic color, with some darker areas at the outermost part of the forelimb pouches and one small line at the anterior margin of the dorsolateral stripes. The area in between the dorsolateral stripes, which extends to the tail-body junction, is of the same color as the dark areas mentioned beforehand. The dorsolateral and median stripes are clearly discernible on the head and the first half of the body, running on top or parallel to the longitudinal axis. The dorsolateral stripes originate and bifurcate at one point posterior to the nares and run next to the eyes, with a moderate gap on eye level. The whitish median stripe originates in between the eyes, not fusing with the origin of the dorsolateral stripes. Anterior to the eye, the dorsolateral stripes are beige, posterior they are whitish. The hindlimbs and the tail are as beige as the dorsum, spotted with some dark dots. Fins are transparent and spotted with dark dots. The ventral side is beige, spotted with gray dots. The hindlimbs' ventral side is brighter than the dorsal side.

Larval staging. At stage 25, right after hatching, the tadpoles had a surface area of $0.23 \pm 0.09 \text{ cm}^2$. During the transition from stage 25 to 27, where the hindlimb buds were slightly visible, the surface area increased to $0.32 \pm 0.11 \text{ cm}^2$. After 29 to 41 days (median=36 days), half of all larvae had developed a hindlimb bud that was equally

in diameter and length and reached a surface area of $0.81 \pm 0.01 \text{ cm}^2$. Between the stages 28 to 40, the larvae had a surface area of $0.88 \pm 0.06 \text{ cm}^2$. During this development period, the hindlimbs grew, all toes became separated and the typical dorsal color pattern was present. The forelimb pouches were discernible after a minimum of 42 and a maximum of 63 days, while half of all individuals reached that development stage after 54 to 58 days (median=56 days). At this point, the tadpoles had a surface area of $1.02 \pm 0.11 \text{ cm}^2$. Not a single larva completed the full metamorphosis to a young froglet (Fig. 6, Table 9). A more detailed staging table based on stereomicroscopic determinations of five specimens from an external source between stages 25 to 37 can be found within the Table 10.

The development was observed under constant conditions with a temperature of 24°C , while the annual mean temperature within the natural distribution area of *R. reticulata* is slightly higher ($T_{\text{Mean}}=24.8^\circ\text{C}$, $T_{\text{Max}}=28.2^\circ\text{C}$, $T_{\text{Min}}=21.5^\circ\text{C}$; Karger et al. 2017a,b; Fig. 7).

Ranitomeya sirensis (Aichinger, 1991)

Breeding behavior in captivity. The breeding pairs among the four specimens deposited clutches of up to two eggs in the bromeliad phytotelm. Reproduction occurred occasionally.

Larval morphology. The description is based on lateral and dorsal pictures of one specimen at stage 29. Thus, no voucher specimen is available. According to McDiarmid & Altig (1999), the tadpole belongs to the exotrophic, lentic, benthic and arboreal larval type. All measurements that were used to calculate the following proportions and its comparison with the other species of this study, can be found in Appendix III.

Dorsal view: Body shape is oval and slightly elongated (MBW/BL=0.86). The snout is short and round (RED/BL=0.24, BWN/BWE=0.88). Nares are oval in dorsal view. The eyes are large (ED/BL=0.09), located dorsally



Fig. 12. Illustrations of the tadpole of *Ranitomeya sirensis*, stage 29 of Gosner (1960). **A.** Frontolateral view. **B.** Lateral view. **C.** Ventral view. Photo credit: Morris Flecks.

Table 11. *Ranitomeya sirensis* (n=31) embryos and hatchlings development stages based on image analyses. Area [cm²] is highly correlated with body mass.

n=31	Stage (n)	Traits	Area [cm²]
Larvae	25 (31)	sinistral spiracle present; oral apparatus clearly visible	0.16 ± 0.04
	25–27 (31)	hindlimb bud slightly visible, length < diameter	0.29 ± 0.13
	28 (15)	hindlimb bud length=diameter	0.58 ± 0.11
	28–40 (15)	hindlimb bud length > diameter; foot paddle slightly visible; indentation between toes 4–5 and 3–4; indentation between toes 4–5, 3–4 and 2–3; Indentation between toes 4–5, 3–4, 2–3 and 1–2; toes 3–5 separated; all toes separated; metatarsal tubercle present; subarticular patches present; hindlimbs with pigmentation; typical dorsal color pattern present	0.86 ± 0.23
	41 (15)	forelimb buds present; typical color pattern on hindlimbs present; lateral stripes present	1.15 ± 0.17
Metamorphs	41–42 (15)	enlargement of the forelimb buds	1.18 ± 0.20
	42 (15)	forelimbs emerged	1.20 ± 0.16
	43 (15)	initiation of tail resorption	1.04 ± 0.16
	43–46 (15)	reduction of the tail until metamorphosis was completed	1.01 ± 0.16

and oriented dorsolaterally. Internarial distance in smaller than interorbital distance (IND/IOD=0.48). Sinistral spiracle is clearly visible in dorsal view.

Lateral view: The body is depressed (MBH/MBW=0.71), the snout is moderately pointed. Nares are almost round. Sinistral spiracle is situated below the longitudinal axis, at the second half of the body (RSD/BL=0.53), oriented laterally with an elliptical opening, whereas the inner wall of the spiracle is free from the body wall. The maximum body height is situated posterior to the spiracle. The tail is long and broadly rounded (TAL/BL=1.90, TAL/TL=0.66). The tail musculature is well developed (TMH/MTH=0.51), “V”-shaped myosepta are visible at the first two thirds of the tail. Both fins are equal in height and originate at the tail body junction. The ventral tube is situated dextrally, the emergence from the abdomen is sagittal and the opening is oval. Hindlimb development is not completed (length ≥ 150% of the diameter). Upper and lower labia are clearly visible in lateral view.

Oral Apparatus: The oral disc is emarginated, elliptical, positioned ventrally and covers more than one third of the maximum body width (ODW/MBW=0.39). Marginal papillae are present at the posterior labium and at the outermost parts of the anterior labium. The anterior labium contains two tooth rows of the same width (A1, A2), with a large gap in the second row (A2-GAP). The posterior labium contains three tooth rows (P1, P2, P3), of which the first has a moderate medial gap (P1-GAP). The first two rows (P1, P2) have the same width, while the third one (P3) is slightly shorter. The tooth row formula is 2(2)/3(1).

Coloration of living tadpole of *R. sirensis*. The basic color is beige, densely covered with dark dots. Two light blue spots anterior to the nares, fused medially (Fig. 12A). The first half of the dorsum is brighter than the second half, additionally slightly transparent below the longitudinal axis (Fig. 12B). Inner organs are visible in ventral and lateral view (Fig. 12C). The hindlimb buds are white, slightly pigmented at the base. The tail has the same coloration as the dorsum, the color density of the dark pigmentation wanes to the posterior end. The tip of the tail lacks any pigmentation. Fins are transparent and spotted with brown dots. The density of those dots decreases to the tip.

Larval staging. During the stages 25 to 27, before the hindlimb buds were clearly discernible, the larvae had a mean surface area of 0.29 ± 0.13 cm² (Table 11). After 24 to 39 days, half of the tadpoles reached stage 28 (median=31 days). At this time, the hindlimb buds were almost equal in width and length and the surface area increased to 0.58 ± 0.11 cm². In between the stages 29 to 40, the hindlimb development was completed and the larvae had a mean surface area of 0.86 ± 0.23 cm². After 47 to 56 days, 50% of the individuals reached stage 41 (median=52 days). The forelimb buds were perceptible and the tadpoles had a surface area of 1.15 ± 0.17 cm². While the forelimbs grew inside the dorsum, the larval growth rate decreased. After 56 to 65 days, half of the tadpoles reached stage 42 and the forelimbs emerged through the body wall (median=60 days). At this time, the tadpoles reached their peak of growth with a surface area of 1.20 ± 0.16 cm². Afterwards, between day 60 and 71 (median=63 days), the resorption of the tail was initiated. Close to the end of the metamorphosis, when the froglets

had just a short remnant of the tail, the metamorphs had a surface area of $1.01 \pm 0.16 \text{ cm}^2$ (Fig. 6, Table 11).

The development was observed under constant conditions with a temperature of $24 \text{ }^\circ\text{C}$, while the annual mean temperature within the natural distribution area of *R. sierrensis* is slightly higher ($T_{\text{Mean}}=24.7 \text{ }^\circ\text{C}$, $T_{\text{Max}}=29.1 \text{ }^\circ\text{C}$, $T_{\text{Min}}=18.8 \text{ }^\circ\text{C}$; Karger et al. 2017a,b; Fig. 7).

Ranitomeya vanzolinii (Myers, 1982)

Breeding behavior in captivity. Successful reproductions were observed in two different terraria, each inhabited by four specimens. While the breeding pairs of the first tank deposited the clutches of two to three whitish to beige eggs in a horizontally orientated and dry film container, the breeding pairs of the second tank placed their clutches of similar size in the bromeliad phytotelm. In rare cases, tadpoles at different development stages were found within the bromeliad phytotelm. Reproduction occurred occasionally.

Larval morphology. The description is based on a single specimen at stage 41 (ZFMK 97361). Further voucher specimens are ZFMK 97369 and 97379. According to McDiarmid & Altig (1999), the tadpole belongs to the exotrophic, lentic, benthic and arboreal larval type. All measurements that were used to calculate the following proportions and its comparison with the other species of this study, can be found in Appendix III.

Dorsal view: Body shape is oval and elongated ($\text{MBW}/\text{BL}=0.76$). The snout is short and moderately pointed ($\text{RED}/\text{BL}=0.23$, $\text{BWN}/\text{BWE}=0.65$). The shape of the nares is not visible in dorsal view. A skin fold connects the nares with the anterior margin of the eyes. Eyes are large ($\text{ED}/\text{BL}=0.10$), located dorsally and orientated

laterally. Internarial distance is smaller than interorbital distance ($\text{IND}/\text{IOD}=0.48$). The single sinistral spiracle is not visible in dorsal view.

Lateral view: Body is depressed ($\text{MBH}/\text{MBW}=0.71$), snout is round. Nares are shaped elliptically, located laterally and orientated ventrolaterally. The single, sinistral spiracle is situated below the longitudinal axis, at the second half of the body ($\text{RSD}/\text{BL}=0.61$), and is oriented laterally. The inner wall is free from the body and the opening is round. The maximum body height is situated posterior to the eye. The tail is long and broadly rounded ($\text{TAL}/\text{BL}=1.87$, $\text{TAL}/\text{TL}=0.65$). The musculature is well developed ($\text{TMH}/\text{MTH}=0.54$, $\text{TMW}/\text{MBW}=0.33$). “V”-shaped myosepta are visible along the whole length of the tail, particularly in the second half. At the maximum tail height, the upper fin is nearly double as high as the lower fin. Both fins originate at the tail-body junction. Ventral tube is slightly reduced, dextral, emergence sagittal from abdomen. Hindlimb development is completed. Upper and lower labia are visible in lateral view.

Oral apparatus: The oral disc is elliptical, emarginated, positioned ventrally and covers nearly one third of the maximum body width ($\text{ODW}/\text{MBW}=0.27$). Marginal, transparent and rounded papillae are present at the posterior labium and except of six to seven papillae at the most lateral part, absent at the anterior labium. Submarginal papillae are absent. The anterior labium contains two tooth rows of the same width (A1, A2) with a large medial gap in the second row (A2-GAP). The posterior labium contains three tooth rows (P1, P2, P3) of which the first row has a moderate medial gap (P1-GAP). P2 is slightly shorter than P1, P3 is slightly shorter than P2. Both jaw sheaths are black and serrated, lateral processes of the upper jaw sheath are present and extend barely past

Table 12. *Ranitomeya vanzolinii* (n=13) larvae and metamorphs development stages based on image analyses. Area [cm^2] is highly correlated with body mass.

n = 13	Stage (n)	Traits	Area [cm^2]
Larvae	25 (13)	sinistral spiracle present; oral apparatus clearly visible	0.19 ± 0.05
	25–27 (13)	hindlimb bud slightly visible, length < diameter	0.32 ± 0.11
	28 (11)	length of the hindlimb bud equal to the diameter	0.53 ± 0.15
	29–40 (11)	hindlimb bud length > diameter; foot paddle slightly visible; indentation between toes 4–5 and 3–4; indentation between toes 4–5, 3–4 and 2–3; Indentation between toes 4–5, 3–4, 2–3 and 1–2; toes 3–5 separated; all toes separated; metatarsal tubercle present; subarticular patches present; hindlimbs with pigmentation	0.76 ± 0.13
	41 (9)	forelimb buds present	0.98 ± 0.09
Metamorphs	41–42 (9)	enlargement of the forelimb buds	1.00 ± 0.10
	42 (9)	forelimbs emerged	1.03 ± 0.11
	43 (9)	initiation of tail resorption	0.92 ± 0.11
	43–46 (9)	reduction of the tail until the completion of the metamorphosis	0.86 ± 0.13

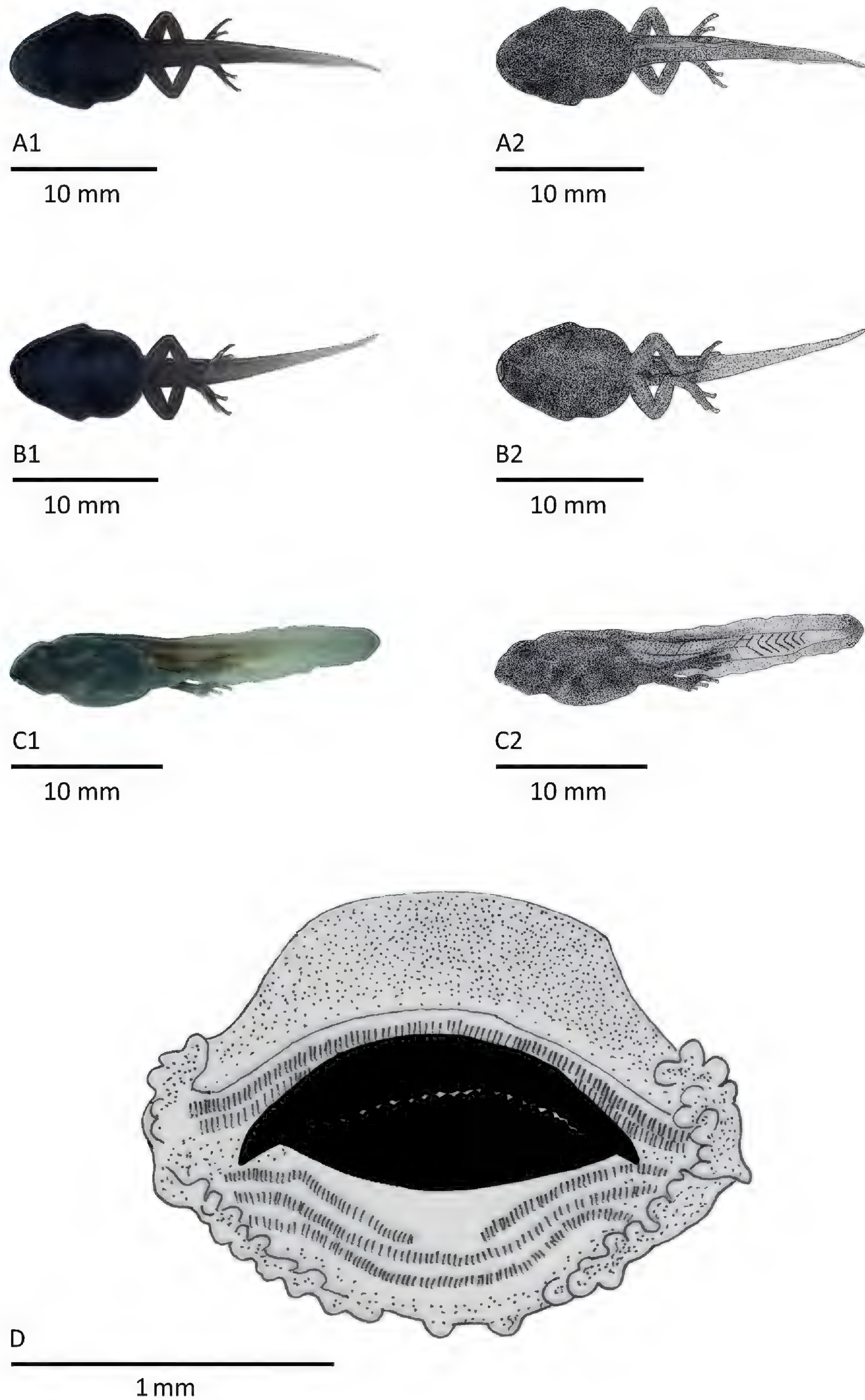


Fig. 13. Illustrations of the tadpole of *Ranitomeya vanzolinii*, stage 41 of Gosner (1960). **A1.** Dorsal view, photograph. **A2.** Dorsal view, drawing. **B1.** Ventral view, photograph. **B2.** Ventral view, drawing. **C1.** Lateral view, photograph. **C1.** Lateral view, drawing. **D.** Drawing of the oral disc. LTRF = 2(2)/3(1).

the lower jaw sheath. The tooth row formula is 2(2)/3(1) (Fig. 13D).

Coloration of a living tadpole of *R. vanzolinii* (ZFMK 97361). The basic color of the dorsum is dark gray to black and lacks any pattern of another color (Fig. 13A1, A2). Hindlimbs are equally colored. The tail is brighter than the dorsum, with a color gradient between the first and the second half of the tail, whereas the color becomes brighter till the tip. The transparent fins are spotted with dark dots.

Coloration of a preserved tadpole of *R. vanzolinii* (ZFMK 97361). The basic color of the dorsum is anthracite, with some beige spotted areas at the forelimb pouches and the muscle attachment of the tail as well as a light gray area which originates at the tip of the snout and extends to the posterior margin of the eyes. The hindlimbs are of the same color as the dorsum, slightly spotted with beige dots. The tail is beige; the anterior half is darker than the posterior one. Fins are transparent and spotted with gray dots. The ventral side is as anthracite as the dorsal side, slightly spotted with beige dots.

Larval staging. At stage 25, right after hatching, the tadpoles had a surface area of $0.19 \pm 0.05 \text{ cm}^2$. During the transition from stage 25 to 27, when the hindlimb bud was just slightly visible in some rare cases, the tadpoles had a surface area of $0.32 \pm 0.11 \text{ cm}^2$ (Table 12). After 32 to 52 days, 50% of the larvae had reached stage 28. At this time, while the hindlimb bud was as long as wide and therefore clearly discernible, the tadpoles had a mean surface area of $0.53 \pm 0.15 \text{ cm}^2$. In between the stages 29 to 40, the development of the hindlimbs was completed and the larvae had a mean surface area of $0.76 \pm 0.13 \text{ cm}^2$. All toes became separated and the hindlimbs pigmented. After 51 to 73 days (mean=60 days), half of all tadpoles had reached stage 41 (Fig. 6). The forelimb buds were clearly discernible and the larvae had a mean surface area of $0.98 \pm 0.09 \text{ cm}^2$. While the forelimbs grew inside the body, the larval growth rate decreased. After 64 to 94 days (median=73 days), half of the tadpoles reached stage 42 and the forelimbs emerged. At this time the tadpoles reached their peak of growth with a surface area of $1.03 \pm 0.11 \text{ cm}^2$. Afterwards, as a part of the ongoing metamorphosis during the stages 43 to 46, the tail was reduced and the mean surface area decreased to a value of $0.86 \pm 0.13 \text{ cm}^2$ (Fig. 6, Table 12). Altogether, the transition from a free living larva to a metamorph which initiated the resorption of the tail lasted 61 to 107 days, while half of all tadpoles reached that development period after 66 to 91 days (median=77 days).

The development was observed under constant conditions with a temperature of 24 °C, while the annual mean temperature within the natural distribution area of *R. van-*

zolinii is slightly higher ($T_{\text{Mean}} = 24.6 \text{ °C}$, $T_{\text{Max}} = 28.9 \text{ °C}$, $T_{\text{Min}} = 19.6 \text{ °C}$; Karger et al. 2017; Fig. 7).

DISCUSSION

We presented new data on the tadpole morphology and development of six *Ranitomeya* species allowing for the first time the identification of specimens in different developmental stages in a captive breeding setup. The development, as studied herein, strongly coincides with the tadpole staging system provided by Gosner (1960). However, few morphological variations between the herein studied tadpoles and a generalized tadpole at Gosner stage 41 were not compatible with those reported in the literature. We observed a delay among the atrophy of the ventral tube on *R. amazonica* tadpoles as well as a delay among the atrophy of the oral apparatus on *R. vanzolinii* tadpoles. The ventral tube in *R. amazonica* was still fully developed, different from that observed for the tadpoles of the other species studied herein, where the ventral tube was partially absorbed. The tadpoles of *R. vanzolinii* in this study displayed a complete oral apparatus, including all anterior and posterior rows of teeth, different from what is reported in Brown et al. (2011) where the tooth rows of *R. vanzolinii* are irregular at stage 40.

The complete metamorphosis was described for five of the six species studied here, as unfortunately none of the tadpoles of *R. reticulata* completed the full metamorphosis. In *R. amazonica*, a species of the *variabilis* group, the tadpoles needed 91–99 days for the complete metamorphosis. The tree species of the *vanzolinii* group studied herein, namely *R. sirensis*, took 60–71 days, *R. imitator* grew up within 67 days and *R. vanzolinii* needed 66–91 days for the complete metamorphosis. *R. benedicta* of the *variabilis* group needed 114 days for the complete metamorphosis.

Waldram (2008) stated that tadpoles of *R. sirensis* (as *R. biolat*) needed 58 days until they completed the metamorphosis in a natural environment. Herein we observed a difference in relation of these results, where the tadpoles of *R. sirensis*, which were bred at a constant temperature of 24 °C with an artificial food resource needed 60–71 days before the absorption of the tail was initiated. In the natural environment, anuran larvae respond to temperature variation by an alteration of their growth and developmental rates (Alvarez & Niecieza 2002; Smith-Gill & Berven 1979). In our study, all clutches were bred under constant conditions (24 °C) and in equivalent water chemistry and nutrition. However, Kam et al. (2001) noticed that the fluctuations in the temperature of phytotelmata mirrored fluctuations in air temperature and hence the water temperatures in the phytotelms are not likely to be constant. Findings of Poelman et al. (2013) support this assumption, as the water temperatures reported in the studied phytotelms present similar averages as the data

of air temperatures obtained from the CHELSA data set (Karger et al. 2017a,b). It needs to be noted that the nutritional conditions in a natural environment are different from that provided during our study.

However, even if the development of the tadpoles studied herein took place in an environment which is different from natural conditions, our results suggest only small morphological differences compared to other descriptions based on tadpoles collected in the field. Therefore, we suggest that if the temperature in the climatic test chamber mimics as closely as possible the known temperatures within the natural habitats of the species, the pace of larval development is presumably more accurate under artificial conditions as they can be easily standardized.

While the coloration of the eggs can be used to distinguish the *vanzolinii* clade from all remaining groups, the coloration of tadpoles does not allow this. Nevertheless, the typical color pattern and the reticulation of the hindlimbs verify the assignment of the specimens to the genus *Ranitomeya*. The provided pictures, drawings and descriptions of the tadpoles should allow to at least the identification of specimens on genus level, which could be useful to help customs officials to recognize CITES protected animals in earlier development stages and therefore reduce the illegal trade.

Methods criticism: Advantages, limitations and efficiency

Recent studies provide growth rates in order to classify the fitness of a species and therefore predict the effects of changing environmental conditions or biotic factors (e.g., as reviewed by Dmitriew 2011). They are either obtained by length-based measurements, quantified by weight or image-based approaches (Relyea 2004; Davis et al. 2008; Pham et al. 2015). As the body length of the tadpole at Gosner stage 35 or greater is highly correlated with the SVL of the young froglet, growth rates based on the former approach usually end at this point of development, as seen in *Amolops creminobatus* (Inger & Kottelat 1998) (McDiarmid & Altig 1999; Pham et al. 2015). Thus, it implies that the change in body size over time stops as well, although shape changes alter the tadpoles' body mass as well as the surface area during this period. Moreover, repeated measurements of living specimens, either with calipers or integrated eye pieces, are stressful for fragile individuals like tadpoles. Studies based on the latter approach use the surface area of a tadpole as a proxy for its body mass. SAISAQ, the method used in this study to generate growth rates of the tadpoles, was introduced by Kurth et al. in 2014, extending the image-based concept of Davis et al. (2008). Instead of manually analyzing images with software packages like Fovea Pro or ImageJ, the implementation into the open source statistic platform R allows a semiautomatic procession based on stan-

dardized image files. Nonetheless, the capabilities of this method are limited. The emerging forelimbs at Gosner stage 41 may affect the dorsal surface to mass relationship, which could falsify the results of the actual and subsequent stages. Moreover, the calibration of the camera in a fixed angle and distance to the object influences the picture quality. While the surface area is sharp and high in contrast, the depth of field decreases. Thus, staging tables based on those pictures need conspicuous traits, reducing their resolution. Nevertheless, SAISAQ allows to document, quantify and monitor the tadpole development in a time-efficient way, obtaining huge amounts of data which could be used to extend our current knowledge of several anuran species.

In order to maximize the sample size while reducing the mortality rate, documentations of the embryogenesis as well as microscopic determinations of the developmental stages were neglected until the growth rate related data acquisition was done. Species which stopped their reproduction at this time of the study lack these measurements (*Ranitomeya benedicta*, *R. sirensis* and *R. vanzolinii*). Thus, staging tables that allow a comparison of all six species are based on image analyses of the growth rate related photographs, which are less detailed than microscopic examinations. Therefore, further studies should either start with the documentation of detailed staging tables and the embryonic development, or conduct both methods simultaneously to add to the completeness of current descriptions. Additionally, an adjustment of the climatic test chamber in regard to the temperatures of the macro-habitats of the species could prove the statement that specimens develop faster if the artificial environment mirrors their natural conditions.

In times of a global biodiversity crisis and wide spread population declines in amphibians, conservation breeding programs become increasingly important. Our data may provide a baseline for further research how to optimize captive breeding in *Ranitomeya* species. The developmental staging tables and growth rates can be used to compare different husbandry and breeding setups. Furthermore, we hope that the detailed larval descriptions are also useful for the identification of specimens by customs.

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APPENDIX I.

Different camera settings (1–4) with regard to light intensities and ISO-Settings.

Setting	1	2	3	4
Light intensity [%]	50	66	80	100
ISO	1600	1600	1600	100

APPENDIX II.

A brief description of the natural history of the target species of this study

Ranitomeya amazonica Schulte (1999) is a poison dart frog placed in the *variabilis* group of the genus *Ranitomeya* (Brown et al. 2011). The basic color is black, with a yellowish orange pattern of medial, dorsolateral and lateral stripes. Frequently, the black component forms a “Y” on the back, which begins at the anterior margins of the eyes and ends at the cloaca (Fig. 1, green color code). The limbs and the ventral side are teal and dotted with black spots. Known are two widely separate populations of *R. amazonica*: east population, distributed in extreme southern Guyana; eastern French Guiana; region of the mouth of the Amazon in Brazil and west population, distributed in northwestern Amazonian Peru (Loreto), extreme southeastern Colombia (Amazonas) and expected in the adjacent borderlands of Brazil (Frost 2006). In the present study we used data from individuals of the western population (Fig. 1). They inhabit primary and secondary rainforests, limited to sparse stands of stunted

trees (Lötters et al. 2007). Clutches of two to six eggs can be found in water filled leaf axils of those bromeliads (Lötters et al. 2007). Due to continuous doubts concerning the taxonomic validity of *R. amazonica*, the extent of its occurrence as well as the ecological requirements are unknown. Therefore, the IUCN lists this species as data deficient (IUCN 2015).]

Ranitomeya benedicta (Brown et al. 2008), also known as blessed poison frog, is placed within the *reticulata* group of the genus *Ranitomeya* (Brown et al. 2011). The predominant color is black, covered by a blue reticulation. Except for the black spots surrounding the eyes, the head region is red and extends posterior to the shoulders (Fig. 1, light blue color code). In some individuals the black areas around the eyes are medially fused and extend to the tympanum, forming a “W”-shaped face mask. Limbs and the ventral side show the same coloration as the dorsum, whereas the throat region is covered by a black marbling. They are distributed throughout the lowland forests of southern Loreto and eastern San Martín, Peru (Brown et al. 2011). While they primarily occur in

forests which are located 150 m above sea level, some individuals have been sighted in areas over 315–405 m elevation (Brown et al. 2008; von May et al. 2008b). Clutches consist of two to six eggs and can be found within the leaf litter covering the forest floor (Brown et al. 2008). Due to an estimated extent of occurrence of about 19,000 km², declining habitats as well as negative effects of the international pet trade, the IUCN list this species as vulnerable (IUCN 2015).

Ranitomeya imitator (Schulte 1986), also known as mimic poison frog, is placed in the *vanzolinii* group of the genus *Ranitomeya* (Brown et al. 2011). There are three different forms, whereby the study organism was a highland form, which is called the *variabilis* or “two dots” type. The ground color of the dorsal side is teal, covered with large black dots. The nostrils are surrounded by two black dots, which extends to the snout and therefore are responsible for the name “two dots”. The ventral side is grayish blue, while the throat is usually yellowish. The limbs are teal and covered with irregular small black dots. The “two dots” or highland form is distributed in Cordillera Oriental, the east of the Departamento San Martín, Peru, 250–1000 m a.s.l. with temperatures fluctuating between 22–26 °C (Lötters et al. 2007) (Fig. 1). The frogs usually inhabit moist premontane primary and secondary forests, but are also able to live along roads or at the margins of plantations, usually found in vegetation heights between 0.5 and 1.5 m above the ground (Lötters et al. 2007). Clutches consist of one to two white eggs, which are placed in a rolled up leaf (Schulte 1986; Brown et al. 2011). Due to its wide distribution range with many suitable habitats and large populations, the IUCN list them as least concern (IUCN 2015).

Ranitomeya reticulata (Boulenger, 1884) is placed within the *reticulata* group of the genus *Ranitomeya* (Brown et al. 2011). The head and the back are usually copper red to reddish brown, while the limbs, the lower sides and the flanks up to the dorsal and sacral region are covered with irregular sized black spots on a bluish background (Fig. 1, yellow color code). The species is distributed throughout the lowland forests of the Departamento Loreto, Peru, 150–200 m a.s.l. to the province of Pastaza, Ecuador, 200–340 m a.s.l. (Brown et al. 2011). In the vicinity of Iquitos, Departamento Loreto, the frogs occur in syntropy to *R. amazonica* in the “varillales”. While *R. amazonica* is more common in moist environments, individuals of *R. reticulata* can be found more frequently in dryer ones, where they perched in vegetation up to 2 m height. In captivity, clutches of one to five eggs are deposited in dark and horizontal places (Lötters et al. 2007). Due to its wide distribution with presumable large populations, the IUCN list them as least concern (IUCN 2015).

Ranitomeya sirensis (Aichinger, 1991), also known as the Sira-poison frog, nowadays comprises the two former species *R. biolat* and *R. lamasi* and is placed in the *vanzolinii* group of the genus *Ranitomeya* (Brown et al. 2011). The ground color of our breeding group was black, with an orange pattern that consists of five thin stripes. The median and the dorsolateral stripes originate anterior to the margin of the eyes and end at the cloaca and at the margin of the thighs respectively, while the two lateral stripes originate at the tip of the snout in between the nostrils and end next to the dorsolateral stripes (Fig. 1, blue color code). Limbs are sage and covered with black spots. The species is distributed from the Amazonian Basin in central eastern and south eastern Peru (Departamentos Loreto, San Martín, Ucayali, Pasco, Junín, Huánuco, Cusco, Madre de Dios) to the southern part of Brazil (State of Acre) and the northern part of Bolivia (Departamento of Pando) (Brown et al. 2011). They usually inhabit premontane and montane primary and secondary forests at elevations between 250–1560 m a.s.l. with an annual precipitation between 1000–7000 mm (Schulte 1999; von May et al. 2008b; Brown et al. 2011). Depending on the elevation, the species inhabits bromeliads or bamboo forests, but also tolerates modulated habitats such as coffee plantations (Lötters et al. 2007). Due to its wide distribution with presumable large populations in combination with the fact that many habitats are protected, the IUCN list this species as least concern (IUCN 2015).

Ranitomeya vanzolinii (Myers, 1982), also known as the Brazilian poison frog, is a member of the *vanzolinii* group of the genus *Ranitomeya* (Brown et al. 2011). The basic color is black, covered with irregular yellow spots which are sometimes fused to lines, especially close to the eyes and at the flanks, or create a marbled pattern at the ventral side. Limbs are teal and covered with black spots. The throat is yellow, whereas a wide dark line crosses the entire width of the posterior part. The species distribution ranges from central eastern parts of Peru (Departamentos Loreto, Huánuco and Pasco) to western Amazonian parts (Estado Acre) of Brazil (Brown et al. 2011) (Fig. 1). They usually inhabit primary lowland forests at an elevation between 200–400 m, except one locality which is situated in the premontane and moist cloud forests between Río Pachitea and Río Ucayali at an altitude of 1300 m (von May et al. 2008b, Brown et al. 2011). As a tree-dwelling species, specimens can be found on trunks, branches and leaves in heights of up to 4 m, or on the ground (Lötters et al. 2007). Clutches consist of one to two light colored eggs which are produced by the same pair that regularly spawns together (Caldwell 1997; Brown et al. 2011). Although the population trend is decreasing, the IUCN still list them as least concern, because they are widely distributed and the populations are presumed to be large enough (IUCN 2015).

APPENDIX III.

Measurements of six different species of the genus *Ranitomeya*. 1. *R. amazonica*. 2. *R. benedicta*. 3. *R. imitator*. 4. *R. reticulata*. 5. *R. sirensis*. 6. *R. vanzolinii*. Measurements were taken from voucher specimens at stage 41, except *R. sirensis* which was at stage 29. All measurements are given in millimeters [mm]. Abbreviations: BL=body length; BWE=body width at eye level; BWN=body width at nostril level; ED=horizontal eye diameter; END=eye nostril distance; IND=internarial distance; IOD=interorbital distance; MBH=maximum body height; MBW=maximum body width; MTH=maximum tail height; ODW=oral disc width; TAL=tail length; TMH=tail muscle height at base; TMW=tail muscle width at base; TL=total length; RED=rostro-eye distance, from tip of snout to the center of the eye in lateral view; RND=rostro-nasal distance, from tip of snout to the center of the nostril in lateral view; RSD=rostro-spiracle distance.

Species	1	2	3	4	5	6
BL	9.38	9.38	9.69	8.38	6.37	9.00
BWE	5.57	5.00	5.29	4.58	4.33	4.86
BWN	3.14	2.86	3.43	2.96	3.83	3.14
ED	1.13	1.00	0.74	0.80	0.55	0.86
END	1.23	1.00	1.08	1.20	1.06	1.31
IND	1.57	1.43	1.43	1.57	1.05	1.57
IOD	3.00	3.57	3.29	2.93	1.74	3.29
MBH	4.14	4.29	5.15	3.48	3.87	4.86
MBW	7.00	7.29	7.14	5.16	5.47	6.86
MTH	3.71	4.14	4.43	3.07	3.30	4.00
ODW	1.86	2.14	2.14	2.04	2.12	1.86
TAL	18.29	19.29	17.14	13.79	12.10	16.86
TMH	2.14	2.57	2.43	1.64	1.69	2.14
TMW	2.29	2.43	2.29	1.87	1.60	2.29
TL	27.67	28.67	26.84	22.17	18.47	25.86
RED	2.15	1.69	2.08	1.79	1.55	2.08
RND	0.92	0.69	1.00	2.37	0.49	0.77
RSD	6.00	5.23	5.92	5.38	3.40	5.46
MBW/BL	0.75	0.78	0.75	0.62	0.86	0.76
RED/BL	0.23	0.18	0.26	0.28	0.24	0.23
ED/BL	0.12	0.11	0.09	0.09	0.09	0.10
RND/RED	0.43	0.41	0.39	0.40	0.32	0.37
IND/IOD	0.52	0.40	0.46	0.53	0.60	0.48
TMW/MBW	0.33	0.33	0.34	0.36	0.29	0.33
MBH/MBW	0.59	0.59	0.73	0.68	0.71	0.71
TAL/BL	1.95	2.06	1.83	1.64	1.90	1.87
TAL/TL	0.66	0.67	0.65	0.62	0.66	0.65
TMH/MTH	0.58	0.62	0.49	0.53	0.51	0.54
TMW/MBW	0.33	0.33	0.34	0.36	0.29	0.33
ODW/MBW	0.27	0.29	0.31	0.40	0.39	0.27
RSD/BL	0.64	0.56	0.56	0.64	0.53	0.61
BWN/BWE	0.56	0.57	0.65	0.65	0.88	0.65

BHL



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Research article[urn:lsid:zoobank.org:pub:B7F64F10-0047-4E2B-86FF-AC61F1B55D26](https://zoobank.org/pub/B7F64F10-0047-4E2B-86FF-AC61F1B55D26)**Revision of *Monolepta* Chevrolat, 1836 species
from North-East Africa
(Coleoptera: Chrysomelidae: Galerucinae)******Thomas Wagner^{1,*}**¹ *Universität Koblenz-Landau; Institut für Integrierte Naturwissenschaften - Biologie, Universitätsstr. 1,
D-56070 Koblenz, Germany**Corresponding author: Email: thwagner@uni-koblenz.de¹ [urn:lsid:zoobank.org:author:6AF65C9C-246B-41CA-B326-2D93C427CCD1](https://zoobank.org/author/6AF65C9C-246B-41CA-B326-2D93C427CCD1)**VIII. part of the revision of Afrotropical *Monolepta*

**53. contribution to the taxonomy, phylogeny and biogeography of the Galerucinae

Abstract. Here, the species of *Monolepta* Chevrolat, 1836 from North-East Africa are taxonomically revised. From this region, covering the states of Egypt, Sudan, South-Sudan, Ethiopia, Eritrea, Djibouti and Somalia, 15 species are known, seven of them: *M. longiuscula* Chapuis, 1879; *M. postrema* Chapuis, 1879; *M. euchroma* Fairmaire, 1883; *M. nigropicta* Laboissière, 1938; *M. marginethoracica* Laboissière, 1940a; *M. nigrocruciata* Laboissière, 1940b; and *M. gobensis* Laboissière, 1940b are endemic to the Highlands of Ethiopia and Eritrea. Further eight species occur in the region, but have wider distribution in Africa: *M. cruciata* Guérin de Méneville, 1847; *M. lepida* Reiche, 1858; *M. vincta* Gerstaecker, 1871; *M. vinosa* Gerstaecker, 1871; *M. ephippiata* Gerstaecker, 1871; *M. citrinella* Jacoby, 1899; *M. leuce* Weise, 1903; and *M. jeanneli* Laboissière, 1920 with *M. kiwuensis* Weise, 1924 as new synonym. Some species have been revised before, and then only additional collecting data are given here. *Monolepta longiuscula*, *M. postrema* and *M. nigropicta* are revised for the first time. Next to detailed redescription of these species, distribution maps and an identification key are given for all species.

Key words. Taxonomy, revision, lectotype designation, synonymy, Africa, Afrotropical Region, Ethiopian Highlands, distribution map, identification key.

INTRODUCTION

In the last catalogue of the Galerucinae (Wilcox 1973), 180 species of *Monolepta* Chevrolat, 1836 from tropical Africa were listed. Most of these species have been described between 1890 and 1950 (Wagner 2017). With very few exceptions, the descriptions by preceding authors were based on external characters only. The allocation to *Monolepta* and other genera of the “Monoleptites” (Wilcox 1973) was mostly typological. In an ongoing revision of this group, the Afrotropical species of *Monolepta* turned out as polyphyletic, and many species have to be transferred to other groups in the meantime (Wagner 2004, 2017).

After revision of the generotype of *Monolepta*, *Monolepta bioculata* (Fabricius, 1781), and a redefinition of *Monolepta* (Wagner 2007a), seven parts on the taxonomic revision of afrotropical “true” *Monolepta* have been published, six parts according to “coloration types” (Wagner 2000a, b; 2001, 2002, 2003, 2005, 2007b), one with focus of the specific fauna of Namibia (Wagner 2016).

Another peculiar fauna of these beetles with high endemism is found in North-East Africa, in particular in the Ethiopian Highlands. Seven species are endemic to the states of Ethiopia and Eritrea, further eight species occur in both countries and the adjacent states of Egypt, Sudan, Djibouti and Somalia, but have also a wider distribution in Africa. Some of these species been already revised in other parts of the revisions cited above, and here only the diagnosis and an update of collection and distributional data are given. Some of the endemic species are revised here for the first time, including figures on external and genitalic patterns. An identification key for all *Monolepta* species from North-East Africa is given.

MATERIAL AND METHODS

A standard set of figures is given for each species. These include illustrations of the coloration (dorsal view), including the right antenna, where black coloration is indicated by black, yellow coloration by white, and red coloration by dot-shading. In polymorphic taxa more than one

coloration type is figured. Note that usually also transitions between the given coloration types occur, i. e., that only typical and frequently found coloration types are illustrated, but there might be more in some species. The basal four antennomeres of usually two different males and females, dorsal and lateral view of the median lobe including the endophallic structures, and ventral view of the median lobe without the endophallic structures (for classification see Wagner 2000a), the spermathecae of two (if available) different females, and bursa-sclerites of one female are figured. Morphometric measurements were made for external characters. Absolute measurements are: total length from the clypeus to apex of the elytron, length of elytron, maximal width of both elytra (usually in the middle or posterior third of the elytra), and width of pronotum. Relative measurements are: length to width of pronotum, maximal width of both elytra to length of elytron, length of second to third antennomere, and length third to fourth antennomere. The number of specimens measured is given in the description under “total length”. If not stated otherwise, lectotypes are herein designated in order to fix the species identity and to preserve the stability of nomenclature in these taxa according to article 74.7.3. of the Code on Zoological Nomenclature.

The subsequent redescriptions and descriptions are based on labelled specimens from the following collections. Acronyms used and responsible curators in brackets: Bishop Museum, Honolulu (BPBM; A. Samuelson); Natural History Museum, London (BMNH; M. Geiser, M. Barclay); Brigham Young University collection, Provo, Utah (BYUC; Shawn Clark); private collection Ron Beenen, Nieuwegein, The Netherlands (CBe); private collection Jan Bezdek, Brno, Czech Republic (CBz); private collection Anthony Drane, UK (CDr); private collection Uwe Heinig, Berlin, Germany (CHe); private collection Frantizek Kantner, Budějovice, Czech Republic (CKa); private collection Lev Medvedev, Moscow, Russia (CMe); Hungarian Museum of Natural History, Budapest (HNHM; O. Merkl); Institute Royal des Sciences Naturelle de Belgique, Brussels (IRSN; P. Limbourg); Museo Civico di Storia Naturale, Genova (MCGD; R. Poggi); Museo Civico di Storia Naturale, Trieste (MCST; A. Colla); Museo ed Istituto di Zoologia Sistemica, Università di Torino (MIZT; M. Daccordi); Musée National d’Histoire Naturelle, Paris (MNHN; A. Mantillieri); Museum für Naturkunde, Berlin (MNHB; J. Frisch, J. Willers); Musée Royal d’Afrique Centrale, Tervuren (MRAC; M. de Meyer); Museum of Zoology, Helsinki (MZHF; H. Silfverberg); Museo Zoologico “La Specola”, Firenze (MZUF; L. Bartolozzi); Naturhistorisches Museum Basel (NHMB; E. Sprecher-Übersax); Naturhistorisches Museum Wien (NHMW; H. Schillhammer); Naturhistoriska Riksmuseet, Stockholm (NHRS; J. Bergsten); Natuurhistorisch Museum Leiden (NNML; R. de Jong); Senckenberg Deutsches Entomologisches Institut,

Eberswalde (SDEI; L. Behne); National Museum of Natural History, Washington (USNM; A. Konstantinov); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK; D. Ahrens, K. Ulmen); Zoological Institute St. Petersburg (ZISP; A. Kirejtshuk); Zoologisches Institut und Zoologisches Museum der Universität, Hamburg (ZMUH; M. Husemann).

RESULTS

Species endemic to Ethiopia and Eritrea

Monolepta longiuscula Chapuis, 1879

(Figs 1–2)

Monolepta longiuscula Chapuis, 1879: 23.

Type material. *Holotypus*. Female, “Abyss., Raffray / Regione boschiva da Goundet ad Adoua, 1000–2000m, 1873 / 5/8” (MCGD). There is no information on specimen numbers in the original description, and I treat the only available specimen as holotype.

Further material studied. 9 specimens, 5 findings. **Eritrea.** 2 ex., Asmara, 15.00N/38.56E (IRSN, MNHB); 3 ex., Adi-Caie, 14.50N/39.21E, IX.1902, A. Andreini (MZUF). – **Ethiopia.** 2 ex., Abyss., Raffray, coll. G. Allard (MNHN); 2 ex., Adigrat, 14.16N/39.27E, V.1963, Linnavuori (MZHF).

Redescription. *Total length.* 4.00–4.80 mm (mean: 4.60 mm; n = 6).

Head. Yellowish-red to red, vertex contrasting black, labrum red, labial and maxillary palpi yellow. Antennae entirely yellow to reddish-yellow, last two to three antennomeres more brownish, not contrasting black (Fig. 1A). Antennomeres slender, second and third in males significantly broader (Fig. 2A), second and third antennomeres usually of same length, length of antennomeres two to three 1.00–1.14 (mean: 1.07), length of antennomeres three to four 0.32–0.42 (mean: 0.37).

Thorax. Prothorax entirely yellowish-red (Fig. 1A), pronotum small and broad, pronotal width 1.10–1.40 mm (mean: 1.26 mm), pronotal length to width 0.60–0.64 (mean: 0.63), very finely punctured, shining. Elytral coloration predominantly yellow, elytral base, humerus, first third of outer margin including epipleura, and about one third of suture black, with slight subapical enlargement of the black sutural patch (Fig. 1A). Elytra very slender, elytral length 3.00–4.10 mm (mean: 3.60 mm), width of both elytra 1.90–2.50 mm (mean: 2.23 mm), with width of both elytra to length of elytron 0.62–0.70 (mean: 0.66). Scutellum red or black. Meso- and metathorax yellowish, legs yellow to reddish-yellow.

Abdomen. Black, strong contrasting to the yellowish underside of thorax (Fig. 1A).

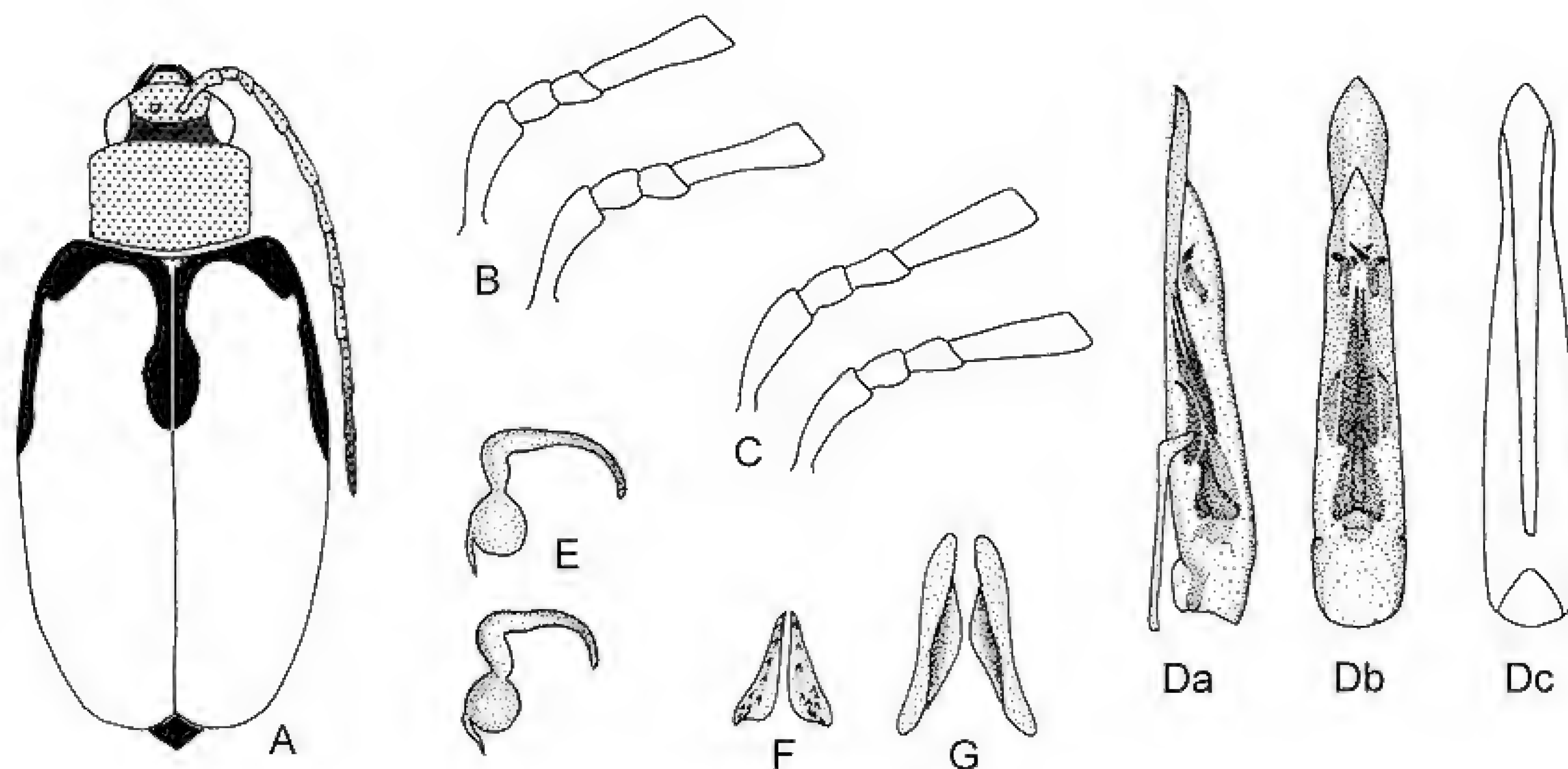


Fig. 1. *Monolepta longiuscula* Chapuis, 1879. **A.** Colour pattern. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Two different spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

Male genitalia. Median lobe slender, conical, significantly narrowed in the apical quarter, with broad and flat apex (Fig. 1D), straight and sometimes with fine setae (Fig. 1Da). Tectum broad, pointed at apex (Fig. 1Db), ventral groove slender, nearly parallel sided (Fig. 1Dc). Lateral endophallic spiculae short, small and characteristically twisted, median spiculae thin and slender, ventral spiculae large with one hook (Fig. 1Db, Dc).

Female genitalia. Spermatheca with small spherical nodulus, slender middle part and long cornu (Fig. 1E). Dorsal part of bursa sclerites slender, sub-triangular (Fig. 1F), ventral part slender triangular, outer margin finely undulate (Fig. 1G).

Diagnosis. In size and body shape most similar to *M. vincta* and *M. ephippiata*. *Monolepta vincta* with reduced transverse elytral band does not occur in North-East Africa, while the most dominant coloration type is with particular broad band (Fig. 15Ac, Ag), median lobe at apex more broad and flat in *M. longiuscula*, dorsal endophallic spiculae of other type (Figs 1D, 15D). *Monolepta ephippiata* with somewhat similar dorsal coloration (Fig. 13Ab), but than at least with median elytral spot, median lobe very different with narrow and pointed apical part and very different endophallic armature (Figs 1D, 13D).

Distribution and ecology. An obviously very rare species collected in the surroundings of Asmara in Eritrea and few adjacent locations of Ethiopia, partly without detailed location data (Fig. 2).

Monolepta postrema Chapuis, 1879

(Figs 3–4)

Monolepta postrema Chapuis, 1879: 22.

Type material. *Lectotype.* Male, “Abyss. Raffray / *Monolepta postrema* Chap. / additional label (added later): Regione boschiva da Goundet ad Adoua, 1000–2000 m, 1893 / Museo Civico di Genova / *Lectotypus Monolepta postrema* Chapuis, 1879” (MCGD). This designation. Chapuis mentioned several specimens in his original publication without designation of a holotype: “De Scio; récolée par M. Antinori à Lit Marefia, en Mai, et à Mahal Uonu en Septembre. Trouvée aussi par M. Raffray entre Goundet et Adoua”.

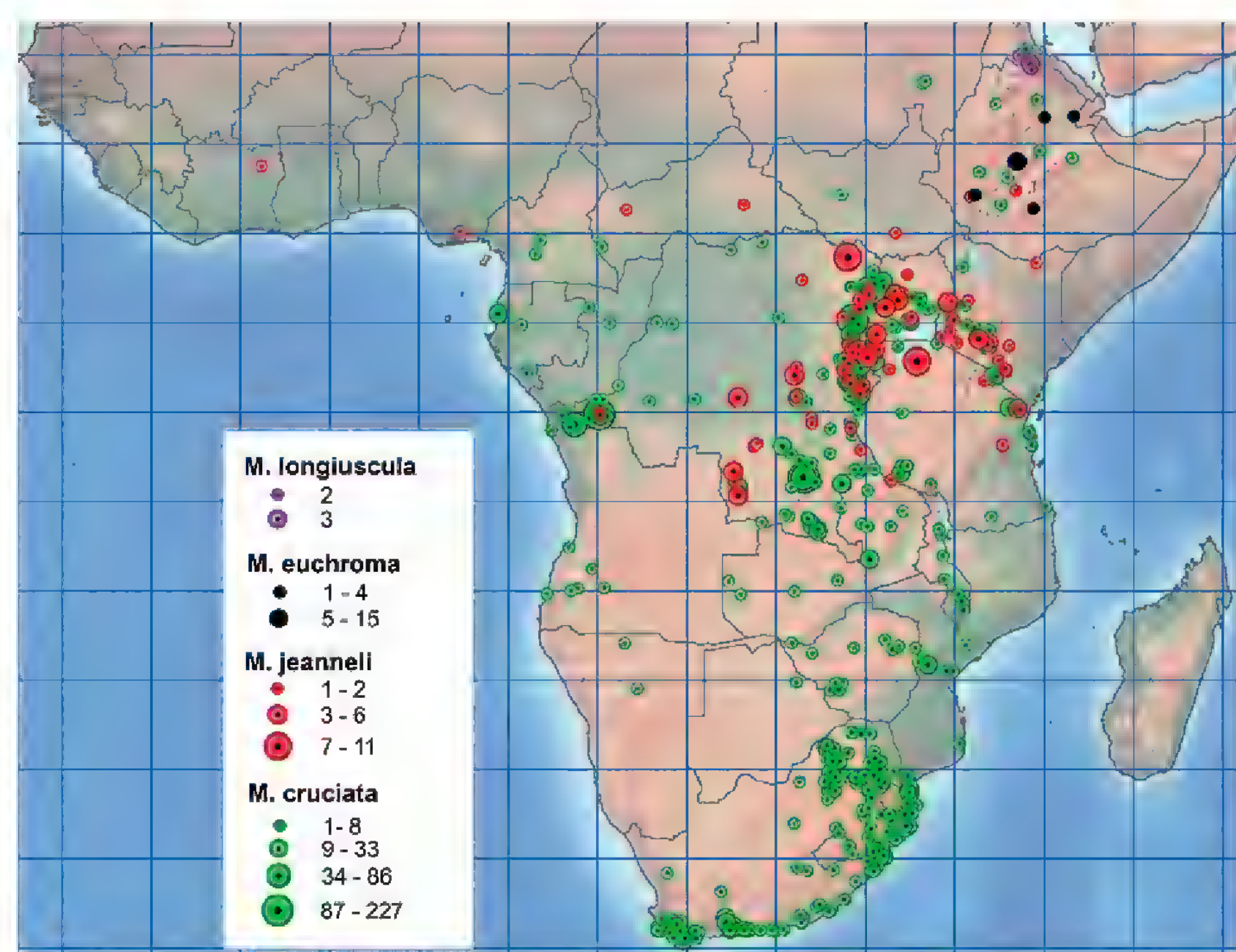


Fig. 2. Distribution of *M. longiuscula*, *M. euchroma*, *M. jeanneli*, *M. cruciata*.

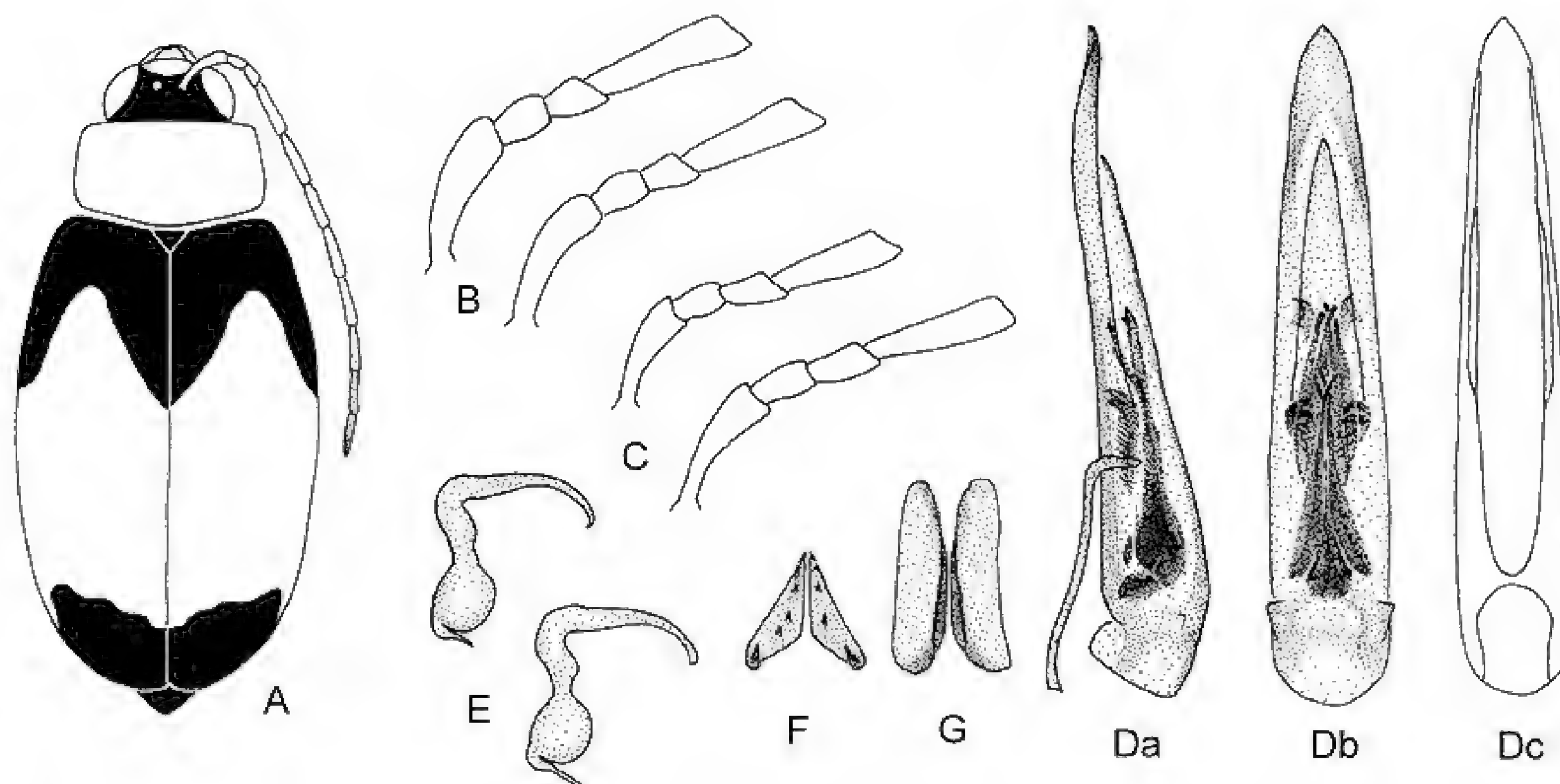


Fig. 3. *Monolepta postrema* Chapuis, 1879. **A.** Colour pattern, **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Two different spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

Paralectotypes. 1 female, same data as lectotype (MCGD); 2 females, Scioa, Lit-Marefia, V.1877, Antinori (MCGD).

Further material examined. 260 specimens, 54 findings. **Eritrea.** 1 ex., Erythree (ZMUH); 1 ex., Asmara, 15.00N/38.56E (MNHN); 1 ex., dto. (HNHM); 2 ex., dto. (NHMW); 4 ex., dto., Chéren, coll. Clavareau (MRAC); 2 ex., dto., Staudinger, ex coll. J. Weise (MNHB); 1 ex., IX.1905, N. Baccari (MCGD); 4 ex., Umg. Asmara, VII.2001, L. & M. Stalmans (IRSN); 5 ex., Ghinda, 15.20N/38.56E (2 ex. MNHB, 1 ex. NMNH, 2 ex. NHRS); 2 ex., Adi-Ugri, 14.53N/38.49E, VIII.1901, IX.1902, A. Andreini (MZUF). – **Ethiopia.** 5 ex., Raffray (MNHN); 2 ex., coll. Chapuis (IRSN); 3 ex., Bogos, coll. Duvivier / Kraatz (2 ex. IRSN, 1 ex. SDEI); 7 ex., Abyssinie, 1881, Raffray (MNHN); 2 ex., Abyssinia, 1928, Mrs. G. McCreag (USNM); 2 ex., Alitiéne, coll. Kraatz (SDEI); 6 ex., Tigre, 1850, Schimper (MNHN); 2 ex., Abyssinia, Tschtscher, VI.1911, Kovács (HNHM); 1 ex., Das, X.1911, R. J. Storley (BMNH); 2 ex., Scioa, Let. Marefia, 6.50N/35.56E, 1881 / VII.1897, Antinori / Ragazzi (MCGD); 3 ex., Addis Abeba, 9.02N/38.42E (ZISP); 6 ex. coll. Le Mout (ZMUH); 33 ex., Dr. Schürhof (MNHB); 1 ex., 1899, Sason (ZISP); 1 ex., VI.1905, M. de Rothschild (MNHN); 1 ex., IX.1926, J. Omer-Cooper (BMNH); 32 ex., 1928, Schürhoff (MNHB); 65 ex., 1930, Schürhoff (MNHB); 5 ex., VII.–IX.1933, L. Sáska (NHRS); 4 ex., X.1948, II.1949, “in flowers of garden roses”, H. Scott (BMNH); 1 ex., Taddese Bogale, V.1956 (USNM); 12 ex., VIII.1963, P. M. Schroeder (NMNH); 4 ex., 2400 m, II.1967, G. M. Shitaye (BMNH); 5 ex.,

II.1972, H. Silfverberg (MZHF); 1 ex., VIII.1988, L. Medvedev (CMe); 1 ex., 2500 m, X.1990, L. N. Medvedev & E. Samoderzhnikov (CMe); 1 ex., II.1995, Bastianini (MIZT); 2 ex., near Adis Allem, 9.01N/38.24E, 2600 m, IX.1926, H. Scott, “cultivated country” (BMNH); 1 ex., Djem-Djem Forest, 2800 m, IX.1926, H. Scott “from grassy open space” (BMNH); 4 ex., Shoa, Wachacha Ravine near Addis Abeba, 2700 m, IX.1926, H. Scott, “from native shrub” (BMNH); 2 ex., between Djem-Djem and Wouramboulchi, 3000 m, X.1926, J. O. Cooper (BMNH); 2 ex., Simien, Derasghie, 3200 m, XII.1952, H. Scott, “from flowering trees & bushes” (BMNH); 1 ex., Belle-ta Forest, 7.32N/36.31E, VI.1963, Linnavuori (MZHF); 1 ex., Agheresalam, 6.29N/38.21E, VI.1963, Linnavuori

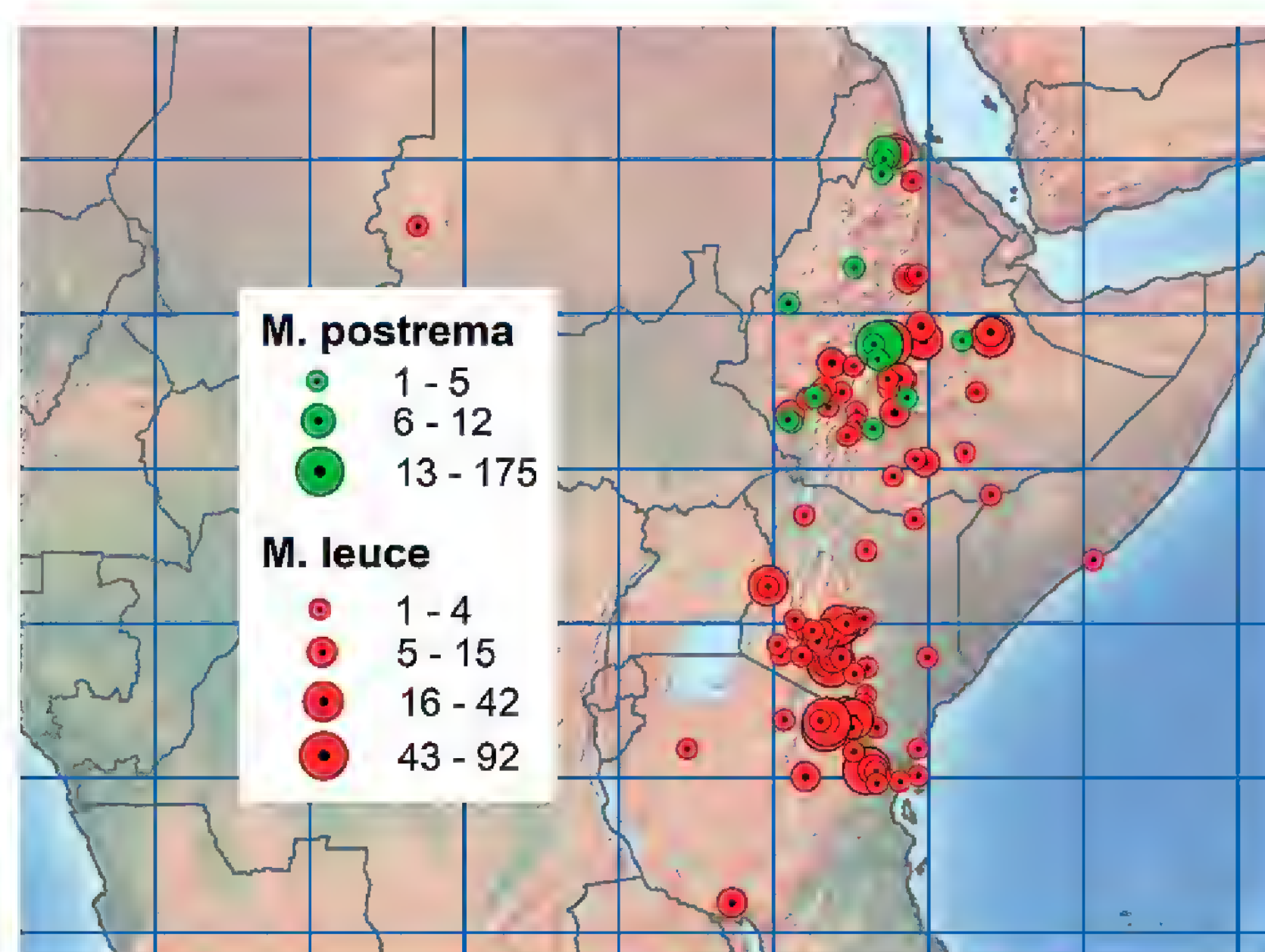


Fig. 4. Distribution of *M. postrema*, *M. leuce*.

(MZHF); 2 ex., Ambo, 7.32N/36.31E, VI.1977, L. Medvedev (CMe); 1 ex., Akaki River, 8.50N/38.43E, XI.1980, sweep-netting, A. Demeter (HNHM); 1 ex., Mt. Menagesha, 8.55N/38.35E, X.1980, sweep-netting, A. Demeter (HNHM); 2 ex., Shewa, 6.58N/35.46E, 1986–1990, Ing. Dedoch (CBz); 1 ex., Debre Zeyt, 10.35N/35.48E, V.1989, K. Werner (MZUF); 1 ex., Ambo/Guder, 2400 m, VII.1990, K. Werner (MZUF); 2 ex., Arsi, Wondo Genet, 7.30N/39.30E, 1850 m, VI.1990, K. Werner (MZUF); 5 ex., Ambo, 650 m, XI.–X.1990, L. Medvedev (CMe); 3 ex., Kaffa Pr., 1850 m, 40 km W Bonga, IV.2007, J. Halada (NME); 1 ex., Amhara Region, Debre Tabor, Debre-sena, 11.51N/37.59E (BYUC); 2 ex., Oromia reg., Hirna, 9.15N/41.08E, 2315 m, V.2011, V. Hula & Niedobova (CBz).

Redescription. *Total length.* 4.80–5.60 mm (mean: 5.20 mm; $n = 16$).

Head. Labrum and frons yellowish, frons sometimes brownish, vertex always black (Fig. 3A), labial and maxillary palpi yellow, terminal palpomeres often brownish. Antennae yellow, usually only last antennomere with brownish to black tip (Fig. 3A). Antennomeres slender, second and third in males significantly broader (Fig. 3B), second and third antennomeres usually of same length, length of antennomeres two to three 0.94–1.15 (mean: 1.02), fourth antennomere usually three times longer than third, length of antennomeres three to four 0.33–0.42 (mean: 0.37).

Thorax. Prothorax entirely yellow, pronotum pale yellow, broad, pronotal width 1.40–1.55 mm (mean: 1.48 mm), pronotal length to width 0.58–0.62 (mean: 0.60), very finely punctured, shining. Elytral coloration characteristic and of constant type, predominantly yellow, black at base, black colour elongated about the first third of the elytra laterally including epipleura and triangle-like along the suture, apical part black (Fig. 3A). Elytral length 3.80–4.40 mm (mean: 4.11 mm), width of both elytra 2.40–2.80 mm (mean: 2.58 mm), slender, width of both elytra to length of elytron 0.59–0.67 (mean: 0.63). Scutellum brownish-red to black. Meso- and metathorax yellow, as legs.

Abdomen. Entirely yellow in about one third of material examined, but mostly yellow with contrasting black anal-sternite and pygidium, rarely also other abdominal segments with darker outer margin.

Male genitalia. Median lobe broad, homogeneously conical (Fig. 3Db, Dc), apex slightly bent dorsally (Fig. 3Da). Tectum small, conical (Fig. 3Db), ventral groove very broad (Fig. 3Dc). Lateral endophallic spiculae short, broad, claw-like, median spiculae and slender, ventral spiculae large, comb-like (Fig. 3Db).

Female genitalia. Spermatheca with small spherical nodulus, broader and long middle part and long cornu (Fig. E). Dorsal part of bursa sclerites slender, sub-trian-

gular (Fig. F), ventral part triangular, outer margin finely undulate (Fig. G).

Diagnosis. Very characteristic by the black basal elytral coloration that is elongated triangularly along the suture. This species shows very low variation in color pattern and can be only dismissed in this respect with *Bicolorizea cavidorsis* (Fairmaire, 1893), that occur sympatrically and is widely distributed in Ethiopia (Heunemann et al. 2015). Also the broad conical aedeagus is a rare pattern in African *Monolepta* species.

Distribution and ecology. Widely distributed and abundant in Ethiopia and Eritrea, particularly in montane regions, recorded up to 3200 m (Fig. 4).

Monolepta euchroma Fairmaire, 1883

(Figs 2, 5)

Monolepta euchroma Fairmaire, 1883: 111.

Further material examined. Ethiopia. 19 specimens, 4 findings. 2 ex., Addis Abeba, Neri, 1941 (USNM); 15 ex., Addis Abeba, 9.01S/38.45E, “roses”, IX.1963, P. M. Schroeder (USNM); 1 ex., Bale, 6.40N/39.40E, IX.2000, P. Leonard (IRSN); 1 ex., Kaffa Pr., 1850 m, 40 km W Bonga, 7.16N/36.04E, IV.2007, J. Halada (NME).

Remarks. A detailed redescription was published in Wagner (2007b). Next to the two type specimens from “Abyssinie A. Raffray Voy. 1881” (MNHN), only ten specimens have been studied of this obviously rare species (Wagner 2007b).

Diagnosis. External and genital characters of this large species are most similar to *M. vinosa* which is obviously phylogenetically closely related. Both species occur sympatrically in the Ethiopian Highlands whereas *M. vinosa* has a much wider distribution covering most regions of the Afrotropis. However, there are some constant differences in detail between both species. The elytral pattern of *M. euchroma* is dominated by the black transverse bands (Fig. 5A), with elytral apex always black but not red margined like in *M. vinosa* with similar predominantly black elytra (Fig. 16A). The female genitalic morphology (spermathecae and bursa sclerites, Figs 5E–G, 16E–G) of both species are not clearly distinguishable, but the median lobe of *M. euchroma* is more slender, the ventral groove is narrow, and lateral endophallic spiculae have a small apical enlargement (Fig. 5D), but not hammer-like as in *M. vinosa* (Fig. 16D).

Distribution and ecology. Only known from few montane sites in the Ethiopian Highlands (Fig. 2).

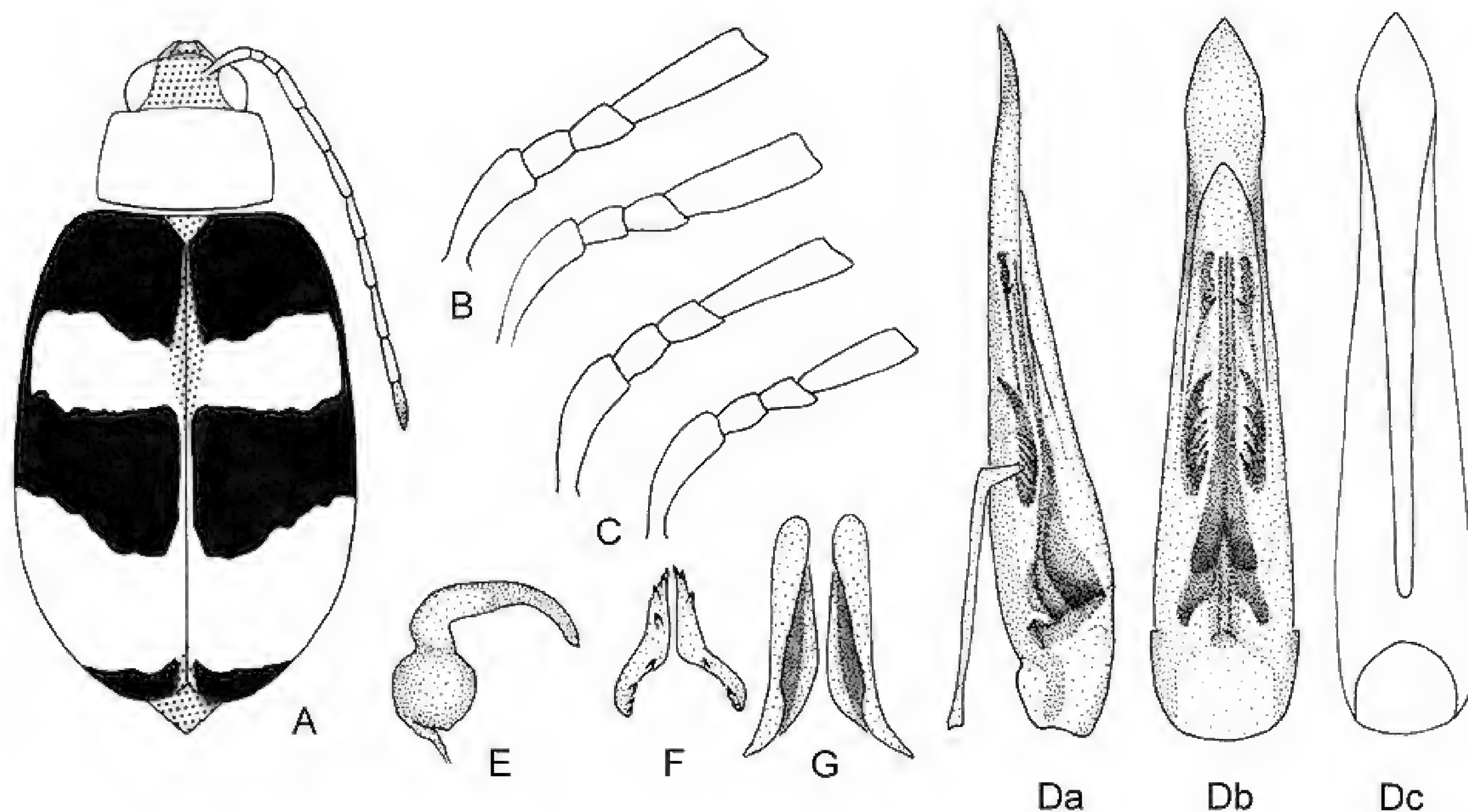


Fig. 5. *Monolepta euchroma* Fairmaire, 1883. **A.** Colour pattern. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

***Monolepta nigropicta* Laboissière, 1938**

(Figs 6–7)

Monolepta nigropicta Laboissière, 1938: 146.

Type material. *Lectotype.* Female, “Da Sancurar agli Amarr, IV.1896, Bottego leg.” (ZMUH); *paralectotype:* 1 female, “Neghelli, Marzo, 1937; Miss. E. Zavattari nei Borana A. O. I.” (MCST). This designation. Laboissière mentioned two specimens in his original description without designation of a holotype “Borana Galla: Sancurar (Bottego 1896), un esemplaire, ma collection; Neghelli, un esemplaire, Zavattari leg. (MCST)”. *Type locality:* Ethiopia, Neghelli, 5.30N/39.05E.

Further material examined. **Ethiopia.** 1 ex., Ethiopie, Sidamo Prov., 14/32 km E of Neghelli, 1600 m, V.1974, R. O. S. Clarke leg. (MRAC).

Redescription *Total length.* 4.60–5.40 mm (mean: 4.90 mm; $n = 3$).

Head. Yellow, vertex contrasting black (Fig. 6A), antenna yellow, only terminal antennomere slightly darker, antennomeres slender, length of antennomeres two to three 0.83–0.86 (mean: 0.84), length of antennomeres three to four 0.42–0.50 (mean: 0.45).

Thorax. Prothorax yellow, broad, pronotal width 1.50–1.65 mm (mean: 1.58 mm), pronotal length to width 0.58–0.62 (mean: 0.60), very finely punctured, shining. Elytra predominately yellow, with narrow black base, an-

terior half of the outer margin, about on ethird along the suture and the elytral tip black (Fig. 6A). Elytral length 3.60–4.20 mm (mean: 3.83 mm), width of both elytra 2.30–2.50 mm (mean: 2.40 mm), elytra slender, width of both elytra to length of elytron 0.62–0.68 (mean: 0.63). Scutellum brown to black. Meso- and metathorax, and legs yellowd.

Abdomen. Yellow, analsternite and pygidium black.

Male genitalia. Median lobe broad, slightly narrowed in the apical quarter (Fig. 6Da), apex broad, flat and straight (Fig. 6Db), tectum broad, ventral groove slender (Fig. 6Dc). Lateral endophallic spiculae slender, bifurcate, median spiculae and slender and bent dorsally, ventral spiculae large with one strong hook (Fig. 6Da, Db).

Female genitalia. Spermatheca with small spherical nodulus, slender middle part and long cornu (Fig. E). Dorsal part of bursa sclerites broad, spiny (Fig. F), ventral part slender, outer margin finely serrate (Fig. G).

Diagnosis. In coloration, size and body shape most similar to some specimens of *M. cruciata* (Fig. 9Ab) and *M. nigrocrucita* (Fig. 13Ab) but not with completely black outer margins. Shape of aedeagus, with broad and flat apical part very different from both other species with slender and conical apical part (Figs 9D, 13D). Somewhat similar to small *M. euchroma* or *M. vinosa*, but those species with partly red elytral coloration, slightly different aedeagus, and very different shape of spermatheca which is slender and long in *M. nigropicta*, and

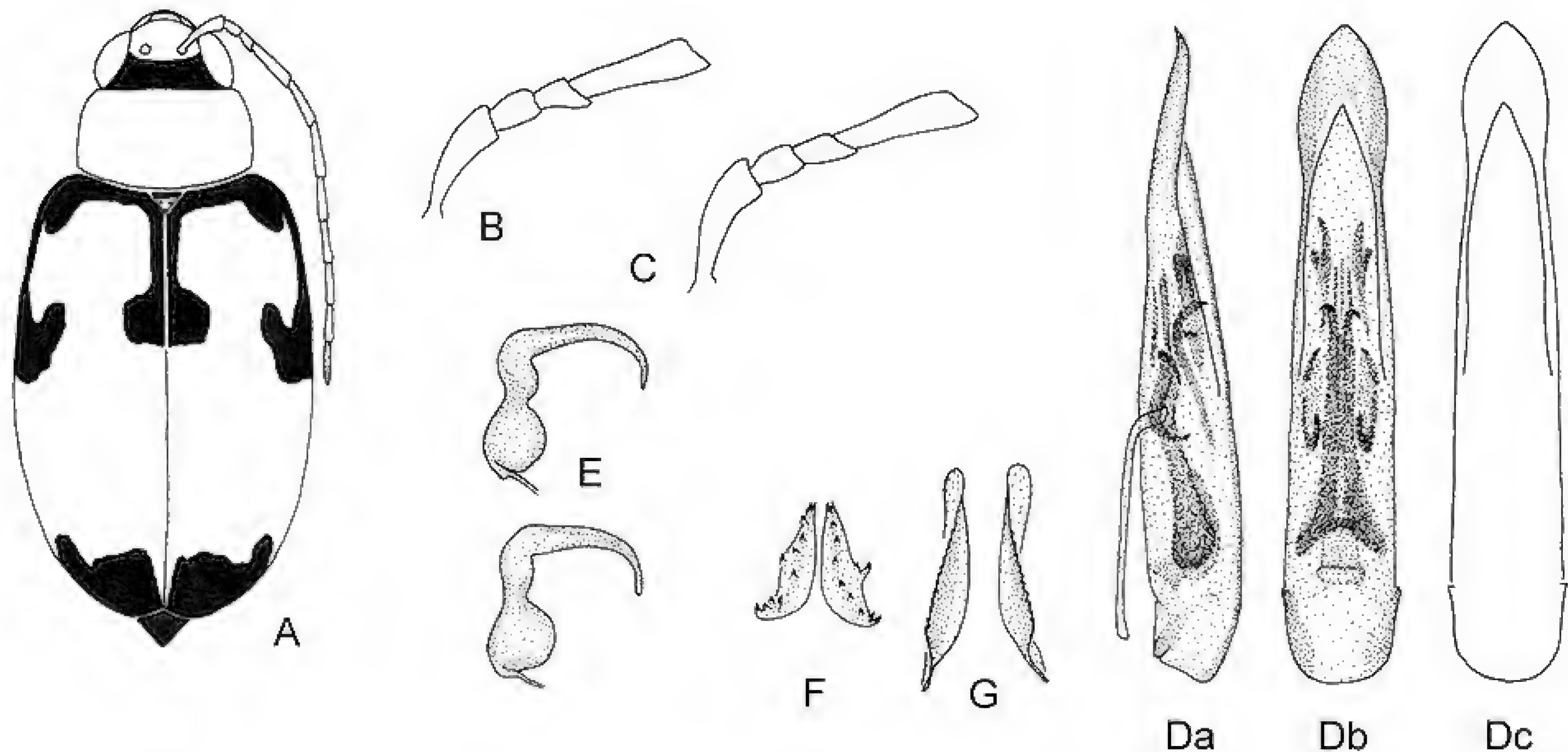


Fig. 6. *Monolepta nigropicta* Laboissière, 1938. **A.** Colour pattern. **B.** Basal antennomere, male. **C.** Dto., female. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

broad with short middle part in *M. vinosa* and *M. euchroma* (Figs 5E, 16E).

Distribution and ecology. Only three specimens are known of this obviously very rare species in Ethiopia (Fig. 7).

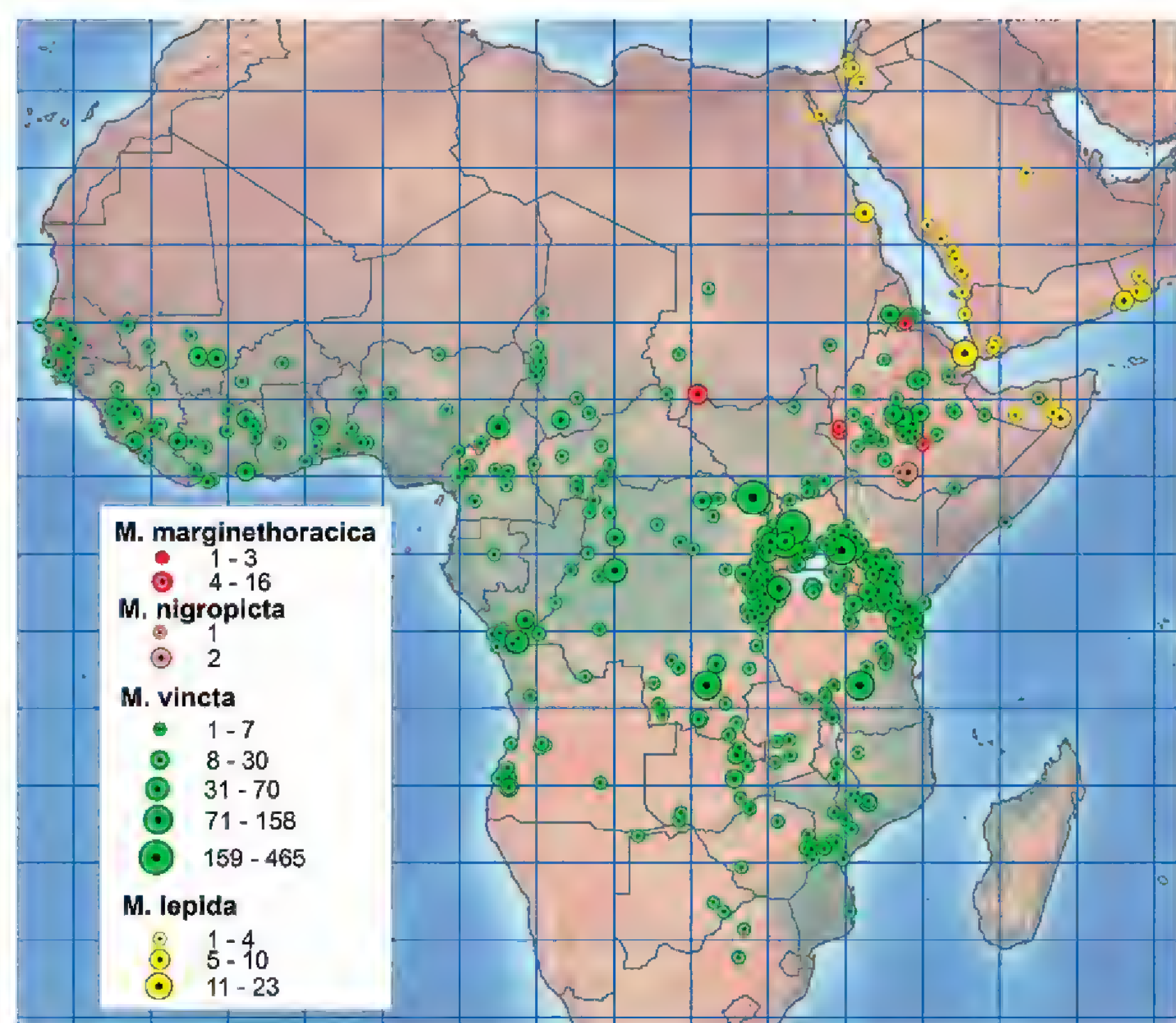


Fig. 7. Distribution of *M. marginethoracica*, *M. nigropicta*, *M. vincta*, *M. lepida*.

***Monolepta marginethoracica* Laboissière, 1940**
(Figs 2, 8)

Monolepta marginethoracica Laboissière, 1940a: 131.

Remarks. A detailed redescription was published in Wagner (2007b). Next to lecto-, and paralectotype “Adi Ugri Eritrea VIII / Musée du Congo Erythrée: Adi Ugri Coll. Clavareau / V. Laboissière det. 1940: *Monolepta marginethoracica* m. Type / R. Det. C 4344” (MRAC), 28 specimens have been revised in Wagner (2007b) and no further specimens have been found afterwards.

Diagnosis. In coloration, external morphometrics and antennal characters most similar to *M. clienta*, but *M. marginethoracica* is on average larger, and has usually completely black margined elytra, whereas the elytral apex of *M. clienta* is red. Both species are allopatrically distributed and can be clearly distinguished by the male genital morphology (Fig. 7D). In size and male genital structures somewhat similar to *M. vinosa*, but can be easily distinguished by the entirely black margined elytra (Fig. 7A).

Distribution and ecology. Only known from few montane sites in Eritrea and Ethiopia. Occurs at the type locality together with *M. longiuscula* Chapuis, 1879, *M. postrema* Chapuis, 1879, and *M. nigrocruciata* Laboissière, 1940 (Fig. 2).

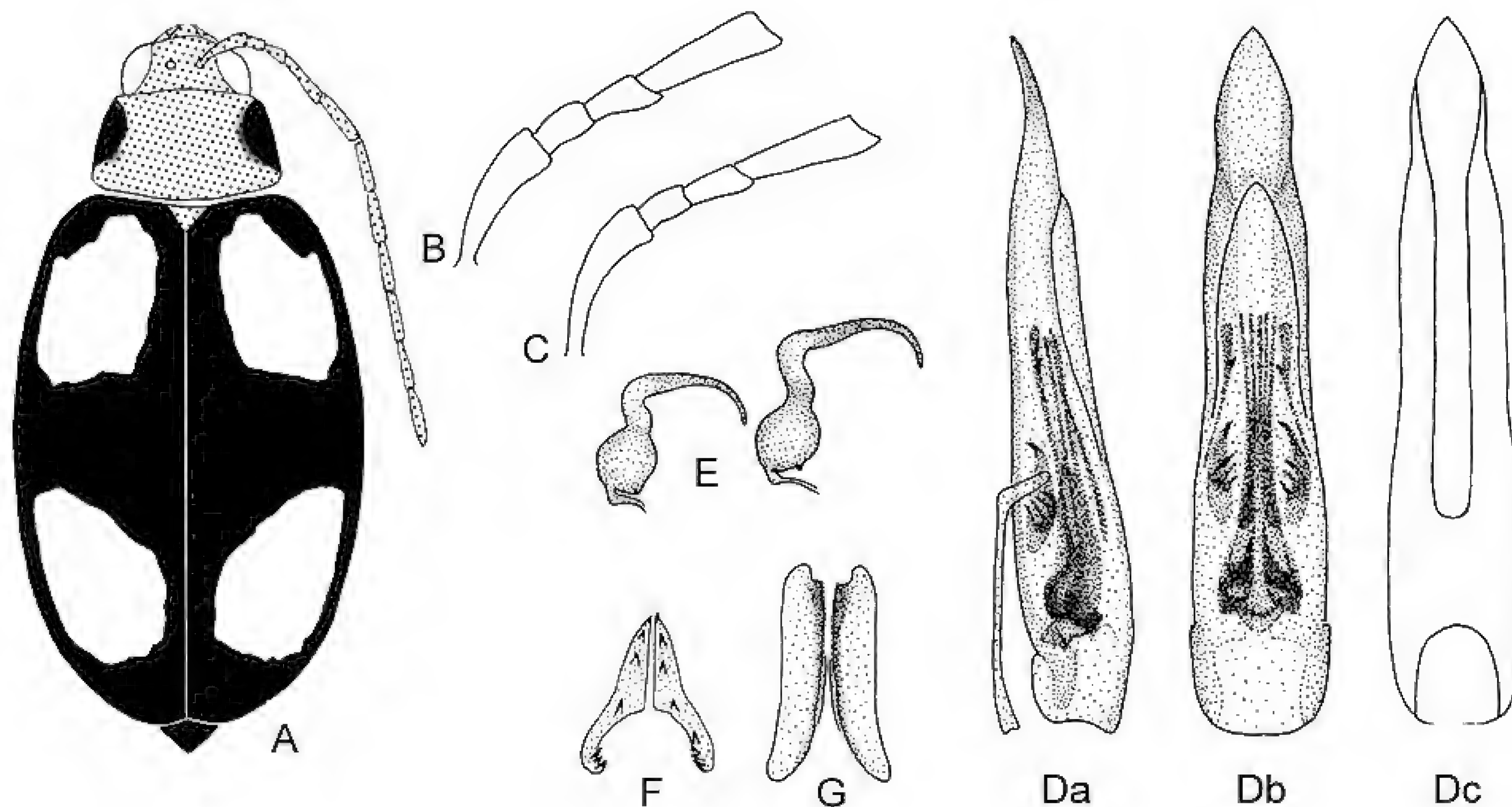


Fig. 8. *Monolepta marginethoracica* Laboissière, 1940a. **A.** Colour pattern. **B.** Basal antennomere, male. **C.** Dto., female. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

***Monolepta nigrocruciata* Laboissière, 1940**

(Figs 9–10)

Monolepta nigrocruciata Laboissière, 1940b: 7.

= *Monolepta varians* Weise, in litteris; Wagner 2007b: 141.

Further material examined. 6 specimens, 2 findings.

Eritrea. 3 ex., Eritrea, Umg. Asmara, VII.2001, L. & M. Stalmans (IRSN). – **Ethiopia.** 3 ex., Addis Abeba, Entono Hill, 9.05N/38.45E, 2840 m, V.2011, Hula & Niedobova (CBZ).

Remarks. A detailed redescription was published in Wagner (2007b). Next to holo-, and 21 paratypes from “Ethiopi Goba R. de Meulenaere 1934–1935 / V. Laboissière det., 1940: *Monolepta nigrocruciata* m. Type / Mus. Hist. Nat. Belg. I.G. 10.738 / cf. Bull. Mus. Hist. Nat. Belg. XVI. 1940 n° 23, p. 7–8, fig. 1 d” (IRSN), 468 specimens have been studied in Wagner (2007b).

Diagnosis. Specimens without elytral cross are most similar to the sympatric *M. gobensis*. The latter has a black pronotum, while specimens of *M. nigrocruciata* without elytral cross and black pronotum are very rare. Furthermore, *M. nigrocruciata* has a broader pronotum (pronotal length to width 0.57–0.63; *M. gobensis* 0.62–0.67) and more slender elytra (width of both elytra to length of elytron 0.62–0.69; *M. gobensis* 0.66–0.71). In any doubtful cases dissection of median lobes and bursa sclerites allow a clear identification of these species in both sexes

(Figs 9D–G, 11D–G). Most similar to *M. nigrocruciata* are some specimens of *M. cruciata* which is also widely distributed in Ethiopia and Eritrea. *Monolepta nigrocruciata* is significantly more slender than *M. cruciata*, but all measured parameters show a more or less wide overlap. Specimens with complete elytral cross (Fig. 9Ac, Ad) should be checked by genital dissection (Figs 9D, 13D–E).

Distribution and ecology. An obviously abundant and widely distributed species of the Ethiopian Highlands and surrounding areas in Eritrea and Ethiopia up to 3300 m (Fig. 10).

***Monolepta gobensis* Laboissière, 1940**

(Figs 11–12)

Monolepta gobensis Laboissière, 1940b: 8.

Further material examined. 2 specimens, 2 findings.

1 ex., Ethiopia, Arussi Prov., Gobe, 10.VIII.1970, S. Persson (NHRS); 1 ex., Oromia, Mt. Enkuolo, NE slope, 7.24N/39.22E, XII.2016, J. Schmidt (NME).

Remarks. A detailed redescription was published in Wagner (2007b). Next to female Holotype “Ethiopi Goba R. de Meulenaer 1934–1935 / V. Laboissière det. 1940: *Monolepta gobensis* m.” (IRSN) Laboissière designated 42 paratypes (all IRSN). 62 specimens listed in Wagner 2007b).

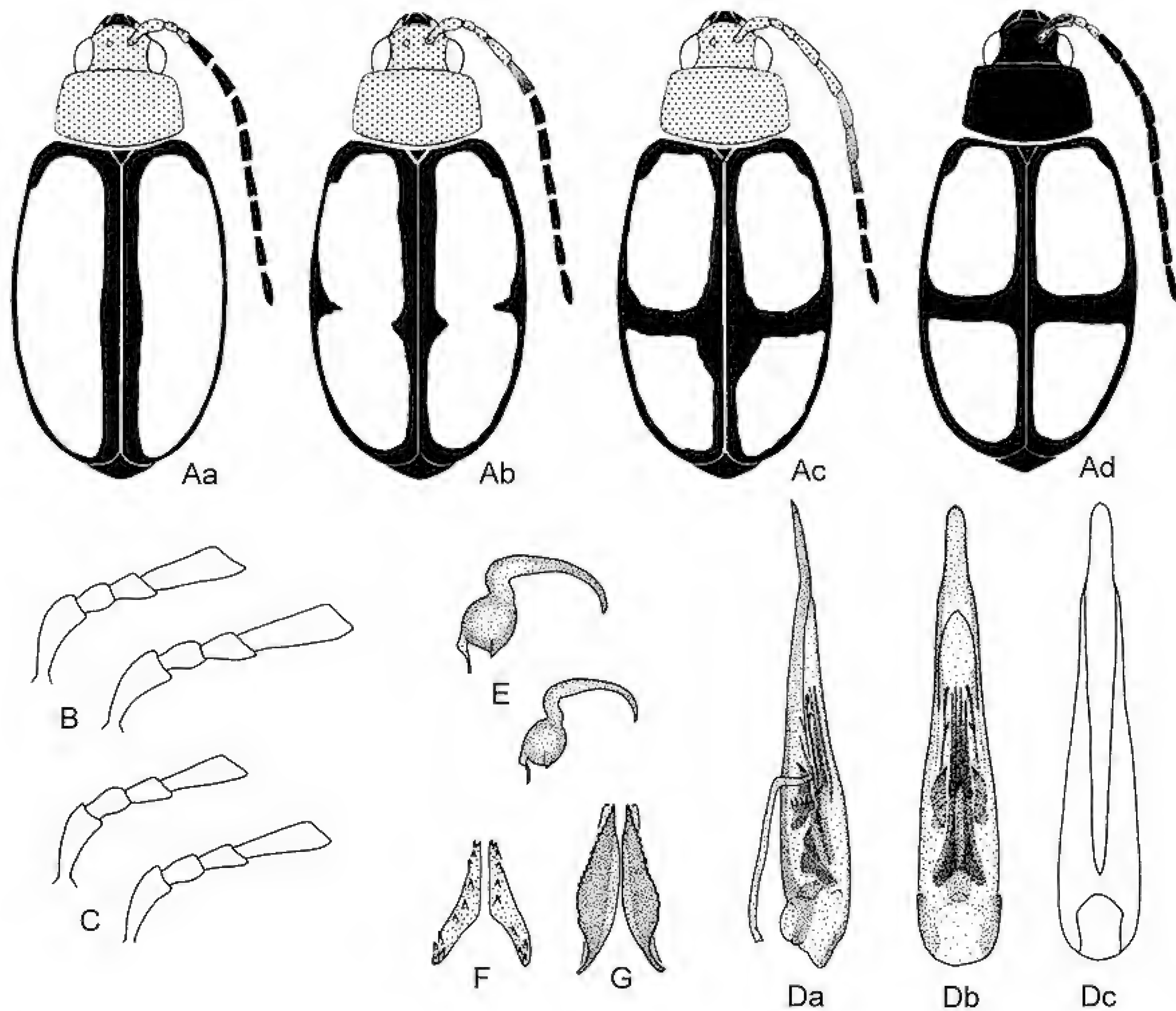


Fig. 9. *Monolepta nigrocruciata* Laboissière, 1940b. **A.** Four different colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

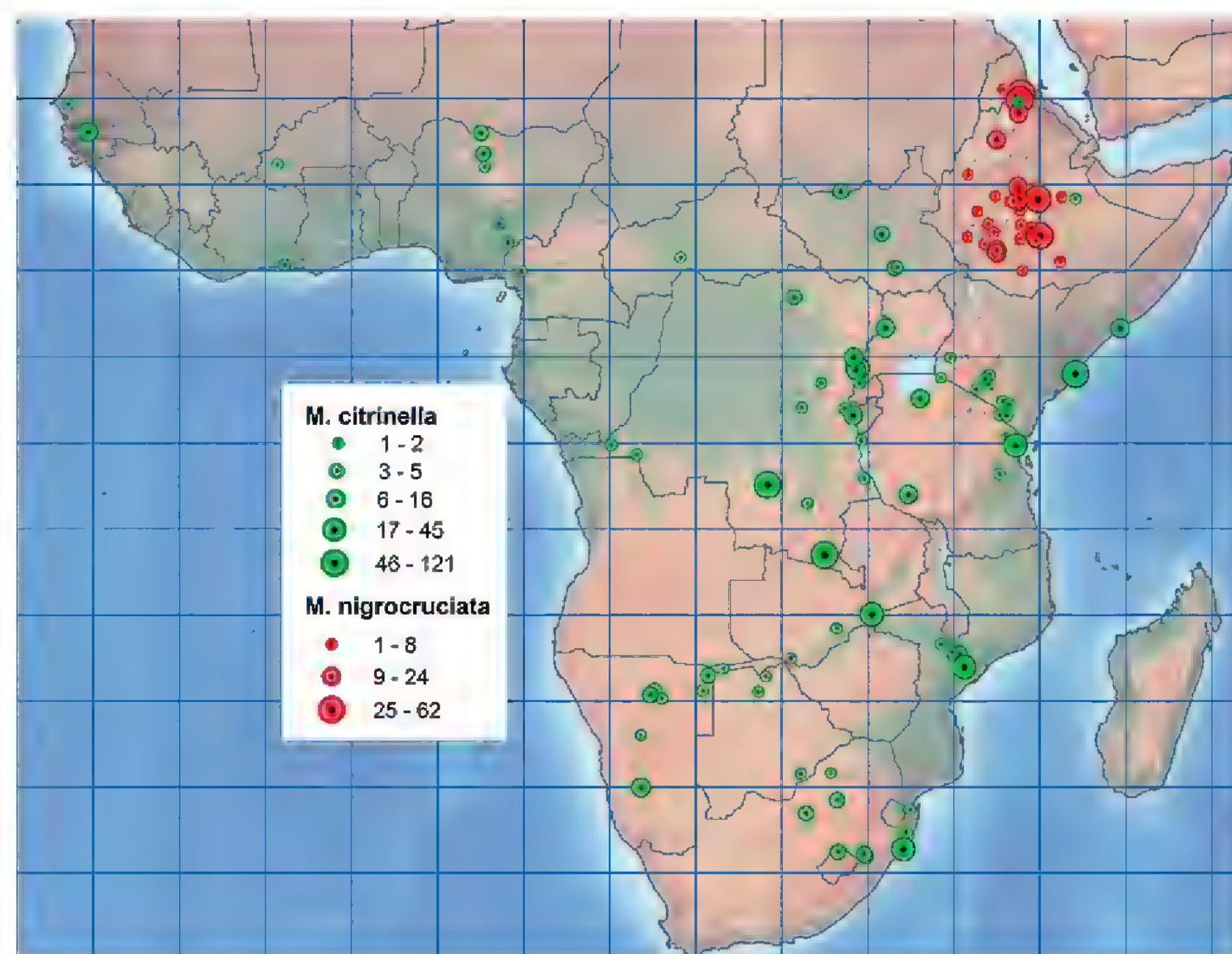


Fig. 10. Distribution of *M. citrinella*, *M. nigrocruciata*.

Diagnosis. Colour pattern without elytral black cross is most similar to *M. deleta*, in particular to specimens from the Usambaras with brownish to black prothorax. Both species occur allopatrically and *M. deleta* particularly in montane regions of Uganda, Kenya and Tanzania. Specimens with elytral cross are very similar to some *M. nigrocruciata* with black prothorax (Fig. 9Ad) that can occur syntopically in Ethiopia. Male genitalia should be dissected in specimens with this coloration to ensure a correct species identification (Figs 9A, 11A).

Distribution and ecology. Restricted to the Ethiopian Highlands in Eritrea and Ethiopia up to 3500 m altitude (Fig. 12).

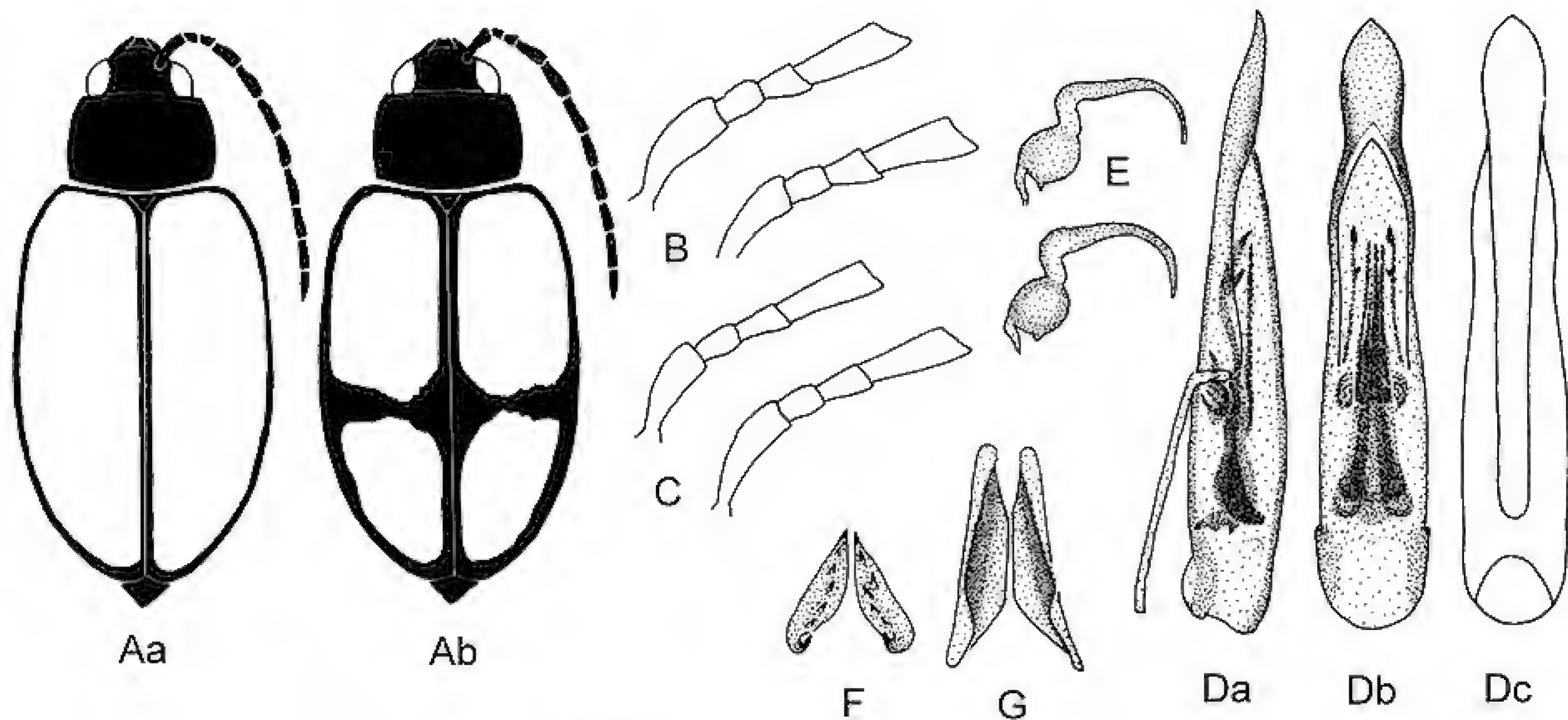


Fig. 11. *Monolepta gobensis* Laboissière, 1940b. **A.** Two different colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

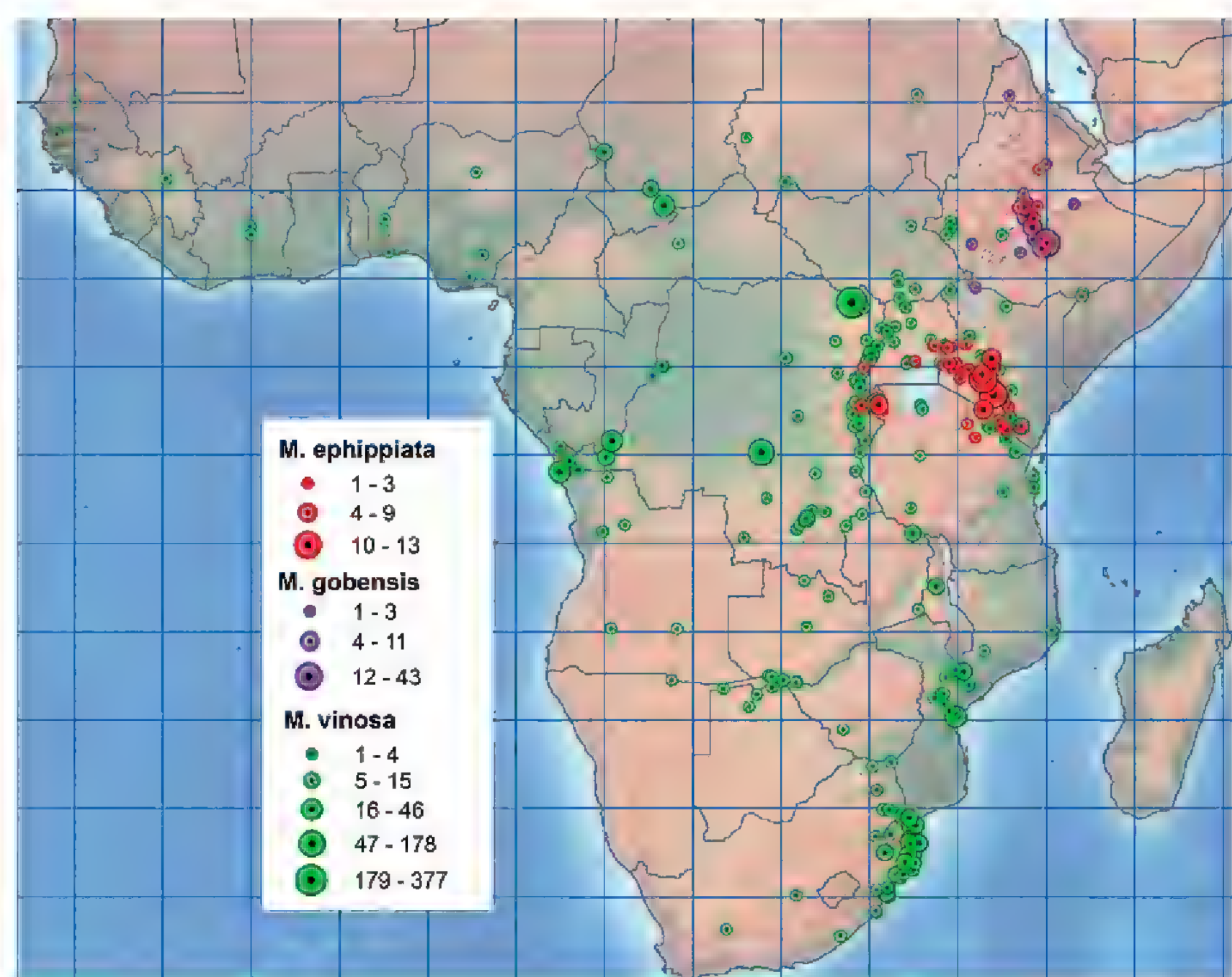


Fig. 12. Distribution of *M. ephippiata*, *M. gobensis*, *M. vinosa*.

Species with wider distribution in North-East Africa

Monolepta cruciata Guérin de Méneville, 1847

(Figs 2, 13)

Monolepta cruciata Guérin de Méneville, 1847: 331.

= *Monolepta puncticeps* Chapuis, 1879: 23; Wagner 2007b: 95.

= *Monolepta ludicra* Weise, 1906: 54; Wagner 2007b: 95.

= *Monolepta sternalis* Weise, 1909a: 213; Wagner 2007b: 96.

= *Monolepta notha* Weise, 1927: 21; Wagner 2007b: 96.

= *Monolepta kivuensis* Laboissière, 1929: 152; Wagner 2007b: 96.

= *Monolepta missis* Laboissière, 1931a: 405; Wagner 2007b: 96.

= *Monolepta carmenta* Weise, in litteris: Wagner 2007b: 96.

Further material examined. 42 specimens, 23 findings. **Angola.** 1 ex. (BMNH). – **Botswana.** 1 ex., Nata, 20.13S/26.11E, XII.1979, C. R. Owen (USNM). – **Ethiopia.** 1 ex., Alemaya, 9.23N/41.56E, VI.1965, A. B. Gurney (USNM). – **Kenya.** 1 ex. Lake Nakuru, 0.28S/36.07E, XI.1896, Dr. Ansorge (USNM); 7 ex., Nairobi, 1.17S/36.50E, XI.1967, C. V. Reichert (USNM). – **Malawi.** 1 ex., Zomba, Upper Shire Riv., 15.21S/35.18E, V.1896, Rendall (USNM). – **Mocambique.** 4 ex., Delagoa Bay, 25.58S/32.35E (USNM); 1 ex., Beira, 19.49S/34.52E (USNM); 2 ex., Lourenço Marques, 25.58S/32.25E, II.1951, N. L. H. Kraus (USNM). – **South Africa.** 2 ex., Durban, 29.51S/31.01E (USNM); 4 ex., Port Natal, 28.30S/30.30E (USNM); 1 ex., Wellington, 33.38S/18.59E (USNM); 1 ex., Grahamstown, 33.17S/26.32E, X.1899, C. le Doux (USNM); 2 ex., Malvern, 26.12S/28.06E, VII.1897 (USNM); 1 ex., Warmbad, 24.55S/28.15E, II.1968, P. Spangler (USNM); 1 ex., Transvaal, Libertas, X.1979, C. R. Owen (USNM). – **Tanzania.** 1 ex., Urambo, 5.04S/32.04E, II.1960, I. A. D. Robertson (BMNH); 1 ex., N-Mara, X.1958, I. A. D. Robertson (BMNH); 2 ex., 30–60 km NE Mpika, 11.40S/31.40E, XI.2004, Snizek (NME). – **Uganda.** 2 ex., Entebbe, 0.05N/32.29E, IX.1972, H. Falke

(USNM); 3 ex., Dokulo, 1.36N/33.10E, XI.1967, C. V. Reichart (USNM). – **Zambia.** 1 ex., Hillwood, Ikilenge, 11.16S/24.18E, X.2013, Smith et al. (BMNH); 1 ex., Lyangu, Liuwa Plain NPO, 14.46S/22.34E, XI.2013, Smith et al. (BMNH).

Remarks. A detailed redescription was published in Wagner (2007b, 2016). Type specimens for the valid name and of *M. puncticeps* originated from Ethiopia. A Neotype was designated for *Monolepta cruciata* in Wagner (2007b). Insect material of the expedition of Th. Lefebvre to Ethiopia was deposited in the MCGD, but type material of this species could not be found. The precise description and the excellent figure given in the original description made an allocation to this species very likely. However, since another species, the sometimes very sim-

ilarly coloured *M. nigrocruciata* occur at the type locality of *M. cruciata*, it was reasonable to designate a neotype to fix the species identity. The lectotype of *M. puncticeps* “Abyss. Raffray / Regione boschiva da Goundet et Adoua, 1000–2000 m 1873” (MCGD) was designated as neotype of *M. cruciata*. *Monolepta cruciata* is one of the most abundant and widely distributed species of *Monolepta* in Africa. Nearly 3000 specimens out of 465 findings have been studied insofar (Wagner 2007b, 2016).

Diagnosis. Specimens with broad black elytral margins, suture and median transverse band (like Fig. 13Aa) are very similar to *M. elegans*. This species has on average more slender elytra and antennae (Wagner 2007a) is abundant only in West Africa, occurs up to Gabon and Angola, and does not occur in North-East Africa. Most

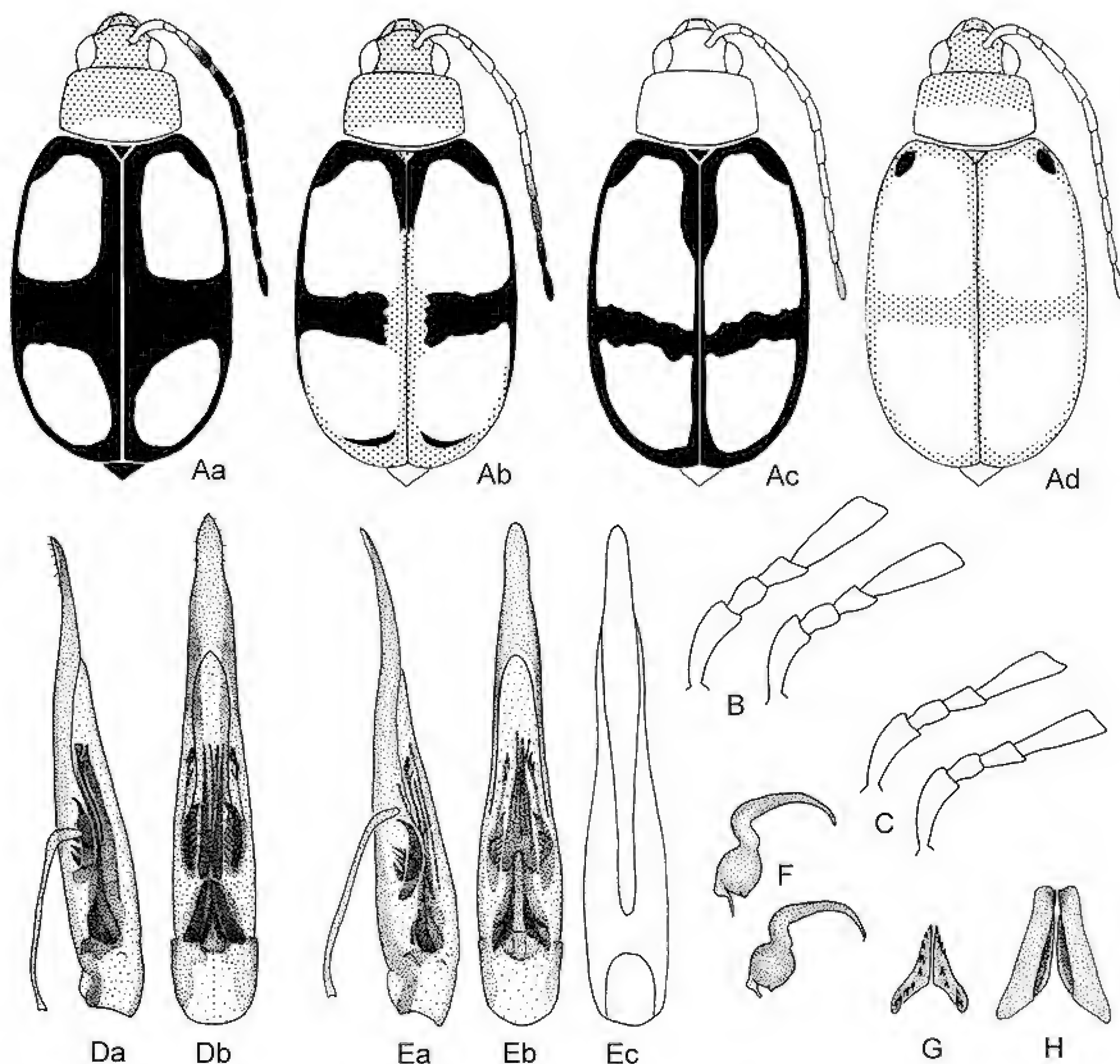


Fig. 13. *Monolepta cruciata* Guérin de Méneville, 1847. **A.** Four different colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal. **E.** Dto., variation a. lateral, b. dorsal, c. ventral, without endophallic structures. **F.** Spermathecae. **G.** Bursa-sclerite, dorsal. **H.** Dto., ventral.

specimens of *M. cruciata* in Ethiopia and Eritrea show colour pattern like Fig. 13Ac, much rarer like Fig. 13Ab. Specimens with complete black suture (Fig. 13Ac) show many similarities to some *M. gobensis* Laboissière, 1940 and *M. nigrocruciata* Laboissière, 1940. Dissection of male genitalia (Fig. 9D, 11D, 13D) is sometimes necessary for proper identification.

Distribution and ecology. One of the most abundant species of *Monolepta* in Eastern, Central and southern Africa from Eritrea and Cameroon to the Cape (Fig. 2).

Monolepta lepida Reiche, 1858
(Figs 7, 14)

Monolepta lepida Reiche, 1858: 263.

Further material examined. 40 specimens, 13 findings. 4 ex., “Arab.”, Ehrenb., 30391 (MNHB). – **Egypt.** 1 ex., Gebel Elba, 22.11N/36.21E, VI.1928, coll. Alfieri (USNM); 1 ex., Oasis Feiran, 28.45N/33.40E, V.1935, coll. Alfieri (NHMB); 3 ex., Wadi Feran, II.–III.1935 Sinai, W. Wittmer (NHMB); 9 ex., Gebel Elba, I.1933, III.1938, H. Priesner (NHMB); 1 ex., Wadi Isla, Bir Tarfa, S-Sinai, 32.00N/34.18E, V.1940, coll. Alfieri (USNM). – **Jordan.** 6 ex., Wadi Schaib, 200 m, XI.1957, J. Klapperich (USNM); 1 ex., 5 km N Mabada, 31.46N/35.48E, IV.1994, Volkovich (USNM). – **Oman.** 1 ex., Dhofar, 18.00N/54.00E, X.1979, T. B. Larsen (USNM). – **Palestine.** 2 ex., Jericho, 31.51N/35.27E, IV.1899, Pic 1899 (MNHN); 4 ex., Wadi Aczajot, Engedi Distr., 31.27N/35.23E, IV.1994, Volkovich (USNM). – **Syria.** 2 ex., Baly coll. (BMNH). – **Yemen.** 5 ex., Jabal al Tark, 16.40N/53.05E, X.2005, M. Rejzek (BMNH).

Remarks. A detailed redescription was published in Wagner (2005). The holotype originates from Jerusalem (MNHN). 72 specimens out of 26 findings are listed in Wagner (2005), and further 58 specimens in 28 findings in Schlich & Wagner (2010).

Diagnosis. Most similar to *M. vincta* and both species occur sympatrically in north-east Africa. Including *M. melanogaster* from southern Africa, these three species are most likely a monophyletic group within *Monolepta* that can be derived from the similarity in external characters, coloration, and male genital patterns. In comparison to *M. vincta*, *M. lepida* is on average larger, and has reduced black elytral coloration (Figs 14–15), while syntopic *M. vincta* often have broad transverse black elytral bands and a black head (Figs. 15Ae, 15Ag, type of *M. alternata* from Ethiopia similar to 15Ac, but with broader transverse black bands).

Monolepta lepida can be distinguished by the elongated second and third antennomeres (length of second to third antennomeres: 0.75–0.88, *M. vincta*: 0.86–1.00; length of third to fourth antennomeres: 0.46–0.54, *M. vincta*: 0.27–0.35) and the narrow pronotum (pronotal length to width: 0.63–0.67, *M. vincta*: 0.57–0.64).

Distribution. Most specimens are known from the Arabian Peninsula and this species is the only one from the Afrotropical Region that reaches the Palaearctic Region in Israel, Jordan, and Syria. Further few specimens are recorded from Eritrea, Somalia, eastern Sudan, and Egypt (Fig. 7).

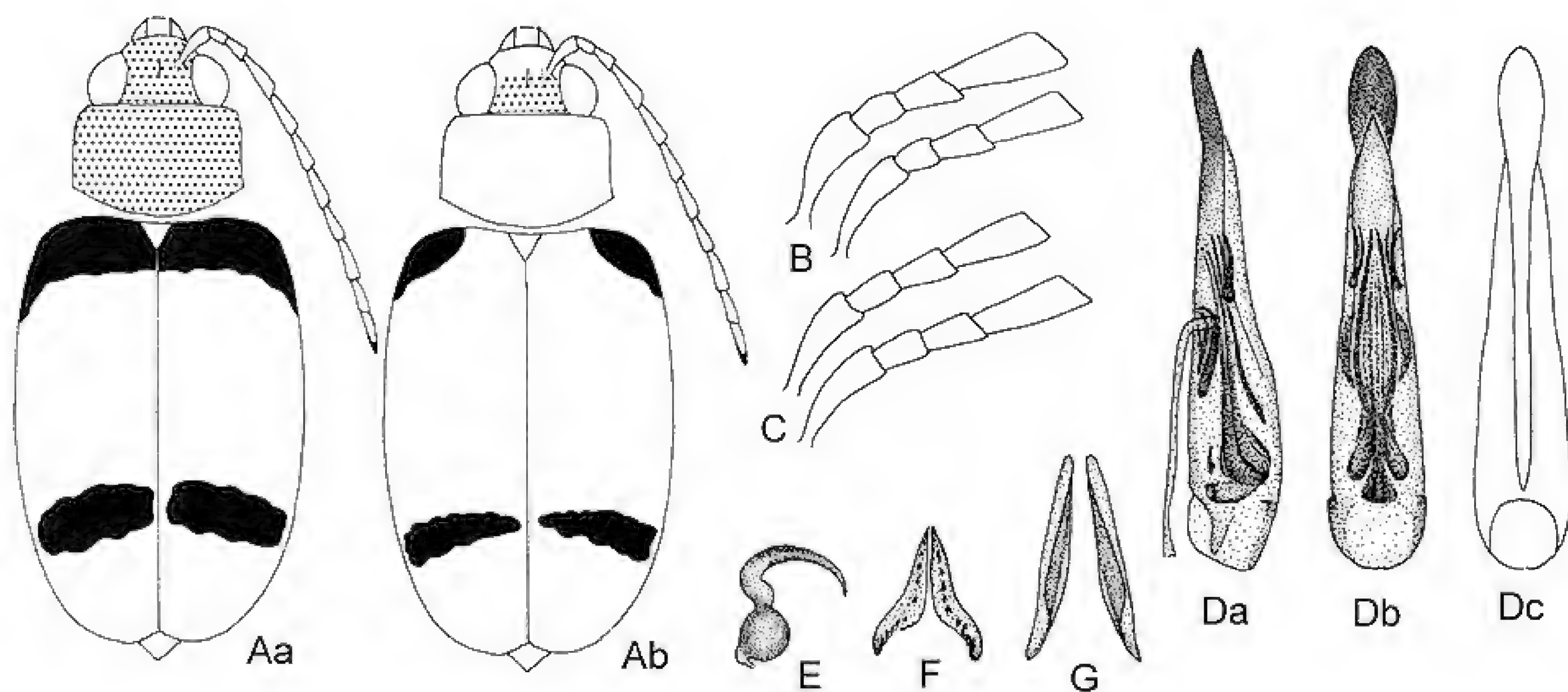


Fig. 14. *Monolepta lepida* Reiche, 1858. **A.** Two different colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

***Monolepta vincta* Gerstaecker, 1871**

(Figs 7, 15)

Monolepta vincta Gerstaecker, 1871: 83.= *Monolepta alternata* Chapuis, 1879: 23; Wagner 2005: 263.= *Monolepta insignis* Weise 1903: 212; Wagner 2005: 263.= *Monolepta sjöstedti* Weise, 1909: 212; Wagner 2005: 263.= *Monolepta ugandaensis* Laboissière, 1920a: 52; Wagner 2005: 263.= *Monolepta lusingensis* Laboissière, 1920b: 98; Wagner 2005: 263.= *Monolepta bouvieri* Laboissière, 1920b: 98; Wagner 2005: 263.= *Monolepta striola* Laboissière, 1920b: 98; Wagner 2005: 263.= *Monolepta consociata* Laboissière, 1920b: 99; Wagner 2005: 264.= *Monolepta rugifrons* Laboissière, 1920b: 99; Wagner 2005: 264.= *Monolepta femoralis* Laboissière 1940b: 66; Wagner 2005: 263.

Further material examined. 160 specimens, 46 findings. **Botswana.** 1 ex., Serowe, 22.54S/26.42E, IX.1987, malaise trap, P. Forchhammer (USNM). – **Ethiopia.** 1 ex., Wallo Prov., 11.30N/40.00E, V.1957, J. E. Lane (USNM); 6 ex., Rock Valley nr. Harar, 9.19N/42.8E, VI.1965, A. B. Gurney, entirely yellow, brownish abdomen, male with narrow brownish elytral base (BMNH). – **Ghana.** 1 ex., Akosombo, 8.16N/3.00E, VI.1973, L. Knutson (USNM). – **Ivory Coast.** 7 ex., Tai NP, 174 m, 5.50N/7.20W, canopy light, III.2017, Aristophanous et al. (BMNH); 6 ex., Mt. Tonkouï peak, 7.27N/7.38W, light, V.2016, Aristophanous et al. (BMNH); 5 ex., Mt. Nimba camp, 7.35N/8.25W, 823 m, V.2016, Aristophanous et al. (BMNH); 1 ex., Kromambira vill., 8.30N/3.37W, 220 m, VIII.2016, Aristophanous et al. (BMNH); 23 ex., Yeale Village, Mt. Nimba, 7.32N/8.25W, IV.2016, Aristophanous et al. (BMNH). – **Kenya.** 1 ex., Chuyulu Hills, 2.35S/37.50E, VI.1938 (USNM); 1 ex., Malindi, 3.13S/40.07E, V.1940, G. W. Jeffery (USNM); 3 ex., Tsavo NP, Kitani Lodge, 3.05S/38.40E, I.1968, Krombein & Spangler (USNM); 3 ex., Amboseli GR, 2.38S/37.14E, I.1968, blacklite, Krombein & Spangler (USNM). – **Liberia.** 1 ex., Mt. Coffee, 6.30N/10.39W, V.1897, coll. O. F. Cook (USNM); 1 ex., Bendija, 1940, W. M. Mann (USNM); 1 ex., Cape Mount, 7.10N/11.00W, 1940, W. M. Mann (USNM); 1 ex., Reputa, 1940, W. M. Mann (USNM); 1 ex., Tropita, IX.1952, on *Citrus*, coll. Blickenstaff (USNM). – **Nigeria.** 3 ex., Olokemeji, 7.20N/4.03E, IV.1936, van Zwaluwenburg & McGough (USNM); 3 ex., Ibadan, 7.23N/3.56E, V.1936, van Zwaluwenburg & McGough (USNM); 1 ex., Gindiri, 9.34N/9.14E, XII.1968 (USNM); 1 ex., Samaru Lake, 11.09N/7.41E, II.1978,

Don & Mignon Davis (USNM); 1 ex., Gashaka Gundi NP, 7.19N/11.35E, IV.2010 (BMNH). – **Sierra Leone.** 5 ex., Tiwai Island, 7.33N/11.21W, 120 m, VI.2016, Takano et al. (BMNH); 1 ex., Outambi-Kilimi NP, 9.40N/12.10W, IX.2009, malaise trap, Takano et al. (BMNH); 1 ex., Njala, 8.00N/10.00W, XI.1916, van Zwaluwenburg & McGough (USNM); 9 ex., Kambana, Moa River, 7.33N/11.05W, VI.2016, light trap, Takano et al. (BMNH); 5 ex., Tiwai Island, Moa River, 7.33N/11.21W, VI.2016, light trap, Takano et al. (BMNH); 5 ex., Loma Mountains, 1050 m, 9.11N/11.05W, VI.2016, light trap, Takano et al. (BMNH). – **South Africa.** 3 ex., Nysvley, 24.29S/28.42E, VI.1976, B. Levey (BMNH). – **South Sudan.** 1 ex., Kajokaji, 3.53E/31.40E, IV.1912, gift ex. MCZ Dupl. Series (USNM); 1 ex., Gilo, 4.02/32.51E, X.1979, A. L. Armstrong (USNM). – **Tanzania.** 1 ex., Lake Manyara, 3.36S/35.56E, 1926, Smithsonian Chrysler Exp. (USNM); 5 ex., Est-Usambara, Amani, IX.2003, Th. Wagner (ZFMK); 26 ex., Kilimamoja, Kibaone, 3.23S/35.49E, IV.2012, Light trap, Smith & Takano (BMNH); 8 ex., Orekeryan, Mt. Longido, 2.43S/36.43E, VIII.2012, light trap, Smith et al. (BMNH); 1 ex., Git-ing, Mt. Hanang, 4.24S/35.24E, 1946 m, XI.2011, Smith & Takano (BMNH); 1 ex., Mt. Meru NP, 3.14S/36.50E, IV.2012, Smith & Takano (BMNH); 1 ex., Ndarakwai, 3.01S/36.59E, 1310 m, IV.2012, Smith & Takano (BMNH); 1 ex., Maskati, Nguru Mits., 6.03S/37.29E, 1759m, X.2010, Smith & Takano (BMNH); 7 ex., Mt. Hanang, 4.24S/35.24E, 2434 m, V.2012, Smith & Takano (BMNH). – **Uganda.** 1 ex., Kampala, 0.19N/32.35E, VI.1940, A. F. J. Gedye (USNM). – **Zambia.** 2 ex., Kalungu, N. of Isoka, 9.41S/32.43E, 1280 m, XI.2016, Smith et al. (BMNH); 1 ex., Lukuli River, Manda NP, 12.15S/30.53E, XI.2012, Smith & Takano (BMNH); 1 ex., Nkwali, S. Lungwa, 13.07S/31.44E, XI.2012, Smith & Takano (BMNH); 3 ex., Greystone, Kitwe, 12.55S/28.14E, 1179 m, XI.2012, Smith & Takano (BMNH). – **Zimbabwe.** 2 ex. Malvern, 26.12S/28.06E, X.1897 (USNM).

Remarks. A detailed redescription was published in Wagner (2005, 2016). The type specimen of the valid name was described from Mombasa, Kenya. One of the numerous synonyms, *Monolepta alternata*, was described from Ethiopia. It is characterized by the black head and broad transversal bands (similar to Fig. 15Ac). One of the most abundant and wide spread species of *Monolepta* in Africa. Up to now (Wagner 2005, 2016) data on 3112 specimens out of 729 findings were studied.

Diagnosis. *Monolepta vincta* is most similar and very closely related to *M. melanogaster* and *M. lepida*. Both species are on average larger, and thus specimens smaller than 3.8 mm total length belong mainly to *M. vincta*. However, there is a high overlap in body size to *M. lepida* which is sympatric to *M. vincta* in North-East Africa.

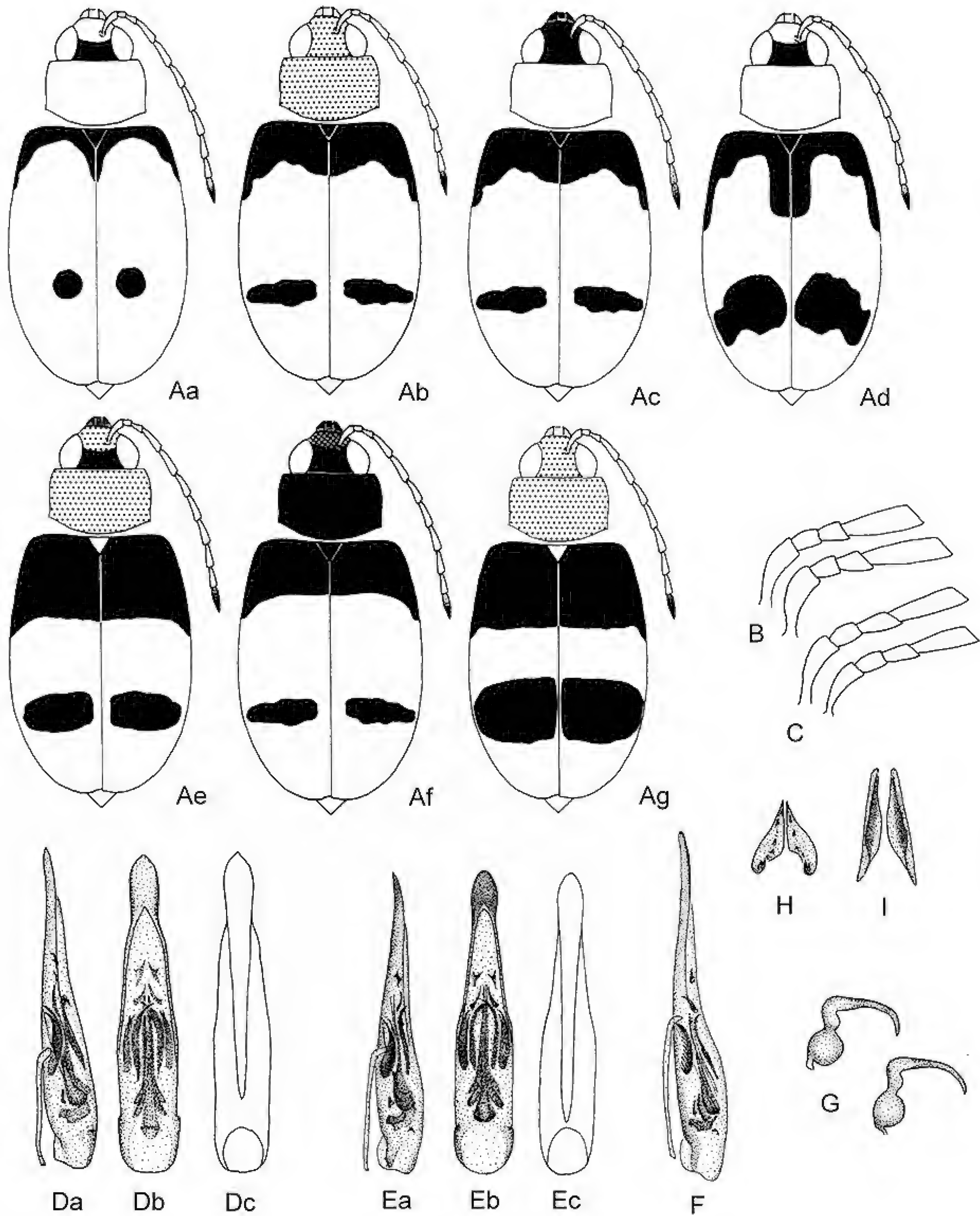


Fig. 15. *Monolepta vincta* Gerstaecker, 1871. **A.** Seven different colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E–F.** Dto., variations. **G.** Spermathecae. **H.** Bursa-sclerite, dorsal. **I.** Dto., ventral.

Next to the male genitalic patterns (Figs 14D, 15D–F), good diagnostic external characters are the lesser elongated second and third antennomeres and the broader pronotum in *M. vincta* (details see diagnosis of *M. lepida*). Other similar species like *M. melanogaster* Wiedemann, 1823, *M. buquetii* Chevrolat, 1836, *M. sharonae* Wagner, 2005, or *M. ronbeeneni* Wagner, 2005 occur only in southern and western Africa.

Distribution and ecology. This species is widely distributed and abundant in most parts of tropical Africa, but with increasing rarity in southern Africa (Fig. 7).

***Monolepta vinosa* Gerstaecker, 1871**

(Figs 12, 16)

Monolepta vinosa Gerstaecker, 1871: 83.

= *Monolepta haroldi* Chapuis, 1879: 22; Wagner 2007: 106.

= *Monolepta buraensis* Laboissière, 1920: 52; Wagner 2007: 106.

= *Monolepta melanocta* Laboissière, 1931b: 45; Wagner 2007: 106.

= *Monolepta neghellia* Laboissière, 1938: 146; Wagner 2007: 106.

= *Monolepta huamboensis* Laboissière, 1939; Wagner 2007: 106.

Further material examined. 27 specimens, 10 findings. **Ivory Coast.** 2 ex., 25 km N Bouake, 7.50N/5.00W, X.1971, black light trap, J. A. Gruwell (USNM). – **Kenya.** 1 ex., Rabur, 0.08S/34.49E, XI.1967, C. V. Reichart (USNM). – **Mocambique.** 12 ex., Delagoa Bay, 25.58S/32.25E, F. C. Bowditch, gift ex. MCZ Dupl. Series (USNM); 1 ex., Beira, 19.49S/34.52E, F. Monros coll 1959 (USNM). – **South Africa.** 1 ex., Durban, 29.51S/31.01E, F. C. Bowditch, gift ex. MCZ Dupl. Series (USNM). – **South Sudan.** 1 ex., Lado Distr., Nimule, 3.36N/32.04E, X.1912 (USNM). – **Tanzania.** 1 ex., Ukiriguru, 2.43S/33.01E, VI.1969, I. A. D. Robertson (BMNH). – **Uganda.** 1 ex., „Lado Distr.“, Wadalai, 2.50N/32.35E, X.1912 (USNM). – **Zambia.** 1 ex., 27 km E of Solwezi, 12.11S/26.30E, XI.2005 (NME); 6 ex., Kalungu, N. of Isoka, 9.41S/32.43E, 1280 m, XI.2016, Smith et al. (BMNH).

Remarks. A detailed redescription was published in Wagner (2007b, 2016). Type specimens for the valid name originated from Northern Tanzania. Two synonyms, *Monolepta haroldi* “Regione da boschiva Goudet ad Adoua 1000–2000 m 1873 / Abyss. Raffray” (MCGD), coloration similar to Fig. 16Ab, and *Monolepta neghellia* “Cotype / Miss. E. Zavattari nei Borana A. O. I. Moralev. 1937” (ZMUH), coloration similar to Fig. 16Aa but with entirely black head, were described from Ethiopia. Up to now 1388 specimens out of 262 findings are revised.

Diagnosis. *Monolepta vinosa* is one of the largest African *Monolepta* species (total length 4.3–7.1 mm), and most specimens with cross-like elytral pattern longer than 5.5 mm belong to this species. The colour pattern of extended black elytral base, entirely red suture, a subapical black spot that is finely reddish margined (Fig. 16Ac) is very characteristic and allows an easy differentiation from all other species. Some specimens with reduced red suture (Fig. 16Ac) are somewhat similar to very few large *M. cruciata* and the syntopic *M. euchroma*. In those specimens a dissection of the genitalia in both sexes with characteristic structures allows a clear differentiation (Figs 5, 13, 16). For more details for *M. euchroma* see there.

Distribution and ecology. One of the most abundant Afrotropical species of *Monolepta*, mainly from savannahs but also known from forest regions (Fig. 12).

***Monolepta ehippiata* Gerstaecker, 1871**

(Figs 12, 17)

Monolepta ehippiata Gerstaecker, 1871: 84.

= *Monolepta sordida* Chapuis, 1879: 23; Wagner 2007: 112.

= *Monolepta ehippiata* var. *keniaensis* Laboissière, 1920: 52; Wagner 2007: 112.

= *Monolepta leakeyi* Bryant, 1953: 866; Wagner 2007: 112.

= *Monolepta turneri* Bryant, 1953: 867; Wagner 2007: 112.

Further material examined. 22 specimens, 10 findings. **Ethiopia.** 1 ex., Oromia reg., Lava fields, nr. Feto, 8.40N/39.29E, 1367 m, V.2011, V. Hula & Niedobova (CBZ); 1 ex., Afar, Metahara, 9.10N/39.51E, 1052 m, V.2011, Hula & Niedobova (CBZ). – **Kenya.** 1 ex., Mt. Elgon, Salt Lake Estate, 1.08N/34.40E, 2100 m, 17.XII.1937, A. Holm (NHRS); 1 ex., Nantuki, 0.01N/37.04E, II.1968, K. V. Krombeim (USNM); 2 ex., Umg. Nairobi, XII.1970, Lichtfang, D. Erber (MNHB); 1 ex., Naro Moru, 0.10S/37.01E, VIII.1978, G. Scudder (BMNH); 5 ex., Lake Naivasha, 0.45S/36.35E, shrub margin, X.2005 (BMNH). – **Tanzania.** 1 ex., Lake Manyara NP, 3.23S/35.52E, XI.2011, Smith & Takano (BMNH); 8 ex., Orekeryan, Mt. Longido, 2.43S/36.43E, VIII.2012, light trap, Smith et al. (BMNH). – **Uganda.** 1 ex., Kakamega Forest, 0.21N/34.52E, VII.2002 (MNHB).

Remarks. A detailed redescription on base of 94 specimens out of 45 findings was published in Wagner (2007b). Type locality of the valid name is Lac Jipe in Northern Tanzania. One synonym from Ethiopia is *M. sordida*, Holotype, #, “Abyss. Raffray / 770 / *Monolepta sordida* Chp / Typus *Monolepta sordida*, 1879 / Regione degli

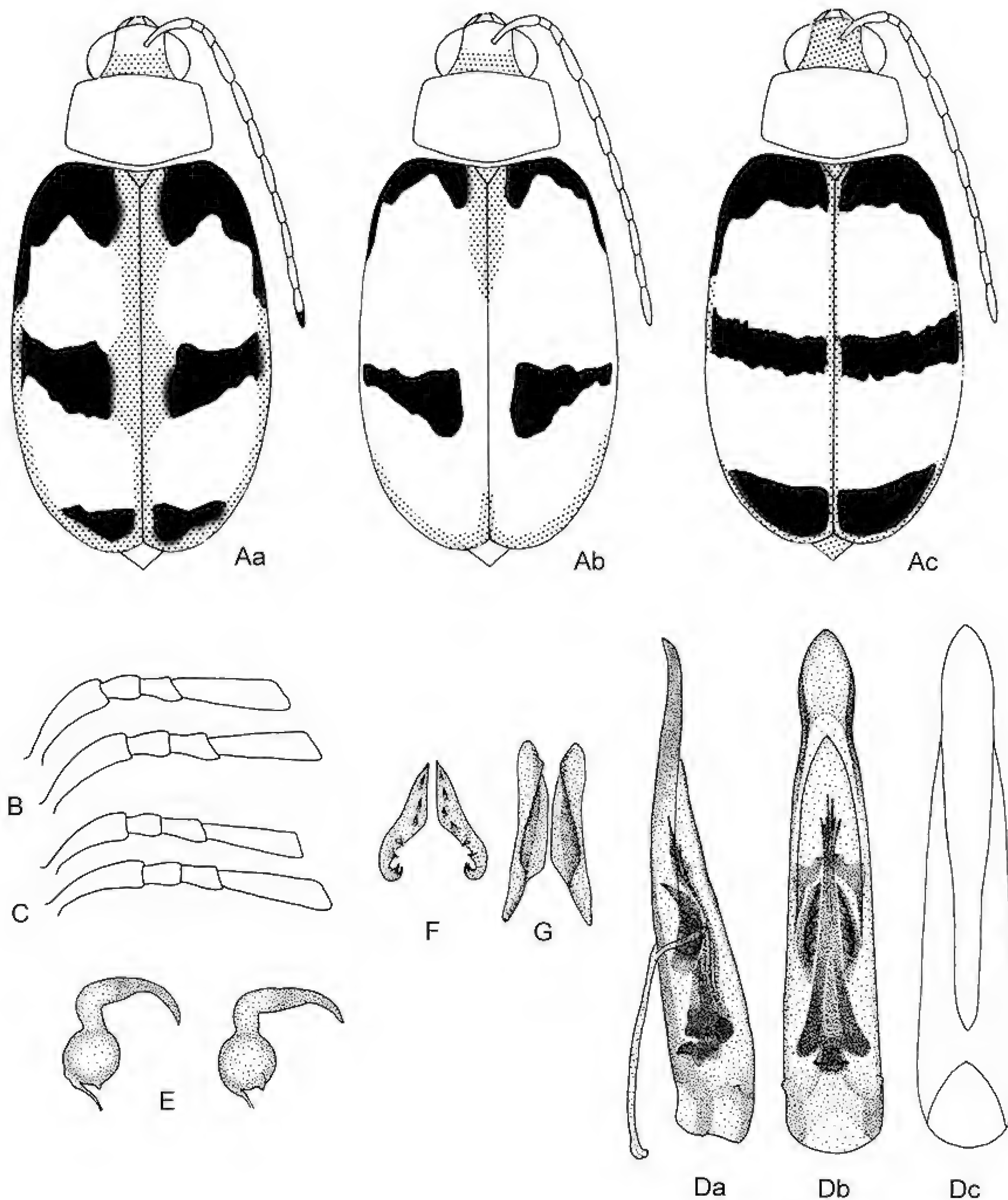


Fig. 16. *Monolepta vinosa* Gerstaecker, 1871. **A.** Three different colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

Agaos XI 1873 Dal fiume Méri Taccazé” (MCGD), coloration similar to Fig. 17Ad.

Diagnosis. A small and slender body with peculiar elytral pattern (Fig. 17A) characterizes *M. ephippiata* and

allow a clear differentiation from all other Afrotropical *Monolepta* species. The apical half of the elytra is usually completely yellow with exception of the elytral tip. Most similar in coloration is the allopatrically distributed

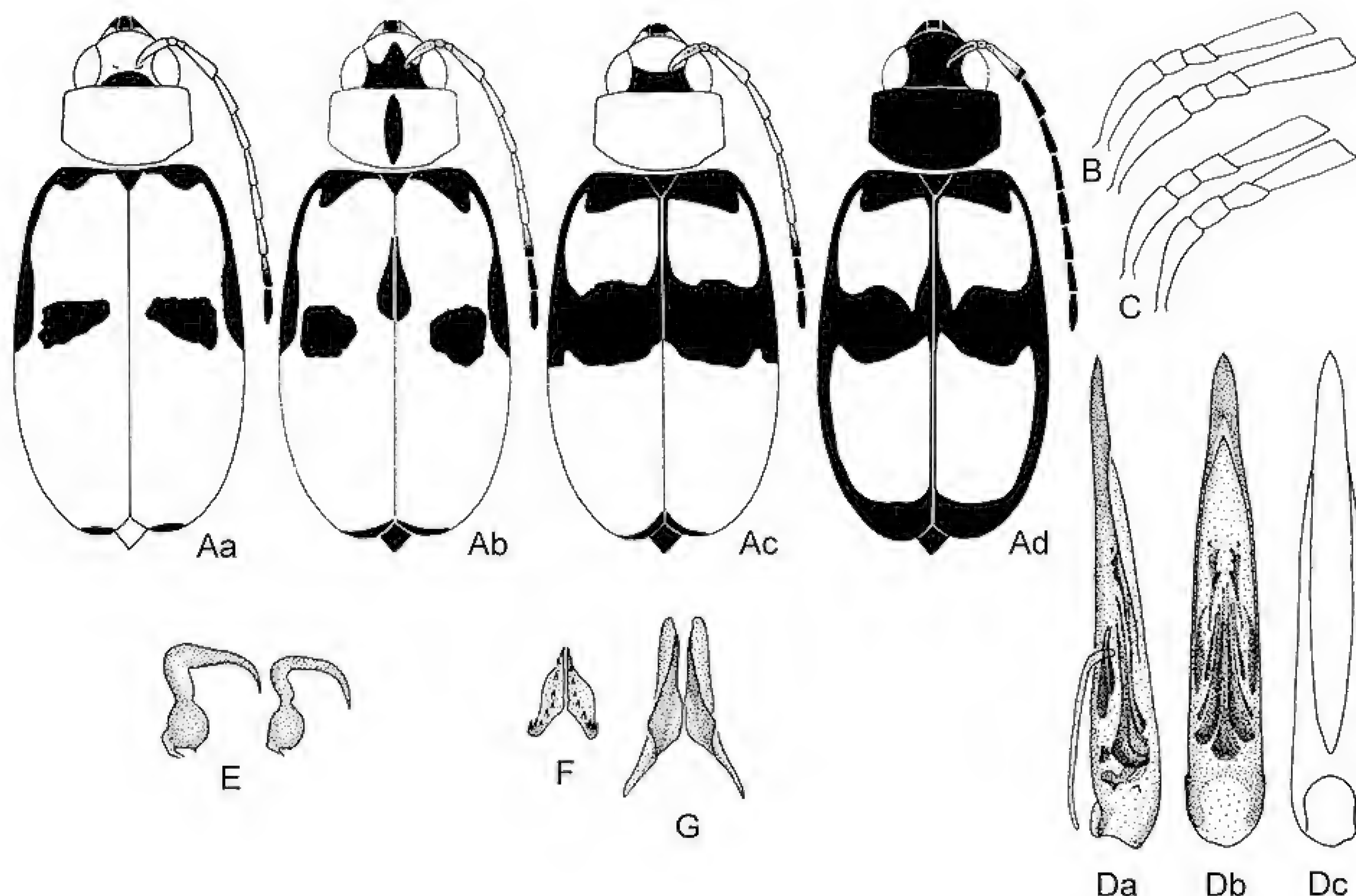


Fig. 17. *Monolepta ehippiata* Gerstaecker, 1871. **A.** Four different colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

M. ehippiatoides Wagner, 2001, which is restricted to southern Africa. It has a more extended black apical elytral coloration, and a reddish head which is contrasting to the yellow pronotum. It is not closely related since the genitalic characters of both sexes are very different from that of *M. ehippiata*.

Distribution and ecology. Restricted to montane areas in East and North-East Africa from Ethiopia through Kenya towards northern Tanzania and Rwanda (Fig. 12). Very abundant in the Rift Valley and the Central Province of Kenya.

***Monolepta citrinella* Jacoby, 1899**

(Figs 10, 18)

Monolepta citrinella Jacoby, 1899: 375.

= *Monolepta michaelsoni* Weise, 1914: 265; Wagner 2016: 424.

= *Monolepta eburnea* Laboissière, 1920: 99; Wagner 2016: 424.

= *Monolepta poriensis* Laboissière, 1920: 100; Wagner 2016: 424.

= *Monolepta oryzae* Bryant, 1948: 62; Wagner 2016: 424.

Further material examined. 24 specimens, 9 findings. **Botswana.** 1 ex., Mochudi, 24.23S/26.09E, XII.1979, C. R. Owen (BMNH). – **Ethiopia.** 2 ex., Rock Valley nr. Harar, 9.19N/42.08E, VI.1965, A. B. Gurney (USNM). – **Mocambique.** 1 ex., Maputo Special Reserve, West Gate, 26.30S/32.43E, VI.2017, Aristophanous et al. (BMNH). – **South Africa.** 4 ex., RSA, NW Prov., Kleksdorf, 26.52S/26.40E, I.2001, Snizek (NME). – **Tanzania.** 7 ex., Ukiriguru, 2.43S/33.01E, IX.1960, I. A. D. Robertson (USNM); 4 ex., Malya, IV.1960, I. A. D. Robertson (USNM); 2 ex., Tarime, 1.21S/34.23E, X.1959, I. A. D. Robertson (USNM). – **Zambia.** 1 ex., Victoria Falls, 17.5S/25.51E, VI.1968, P. Spangler (USNM); 1 ex. Kafue, XII.1919, Univ. Film ex., H. C. Laven (USNM).

Remarks. A detailed redescription was published in Wagner (2016), where 1331 specimens out of 225 findings are revised. The type specimen for the valid name originated from Natal in South Africa.

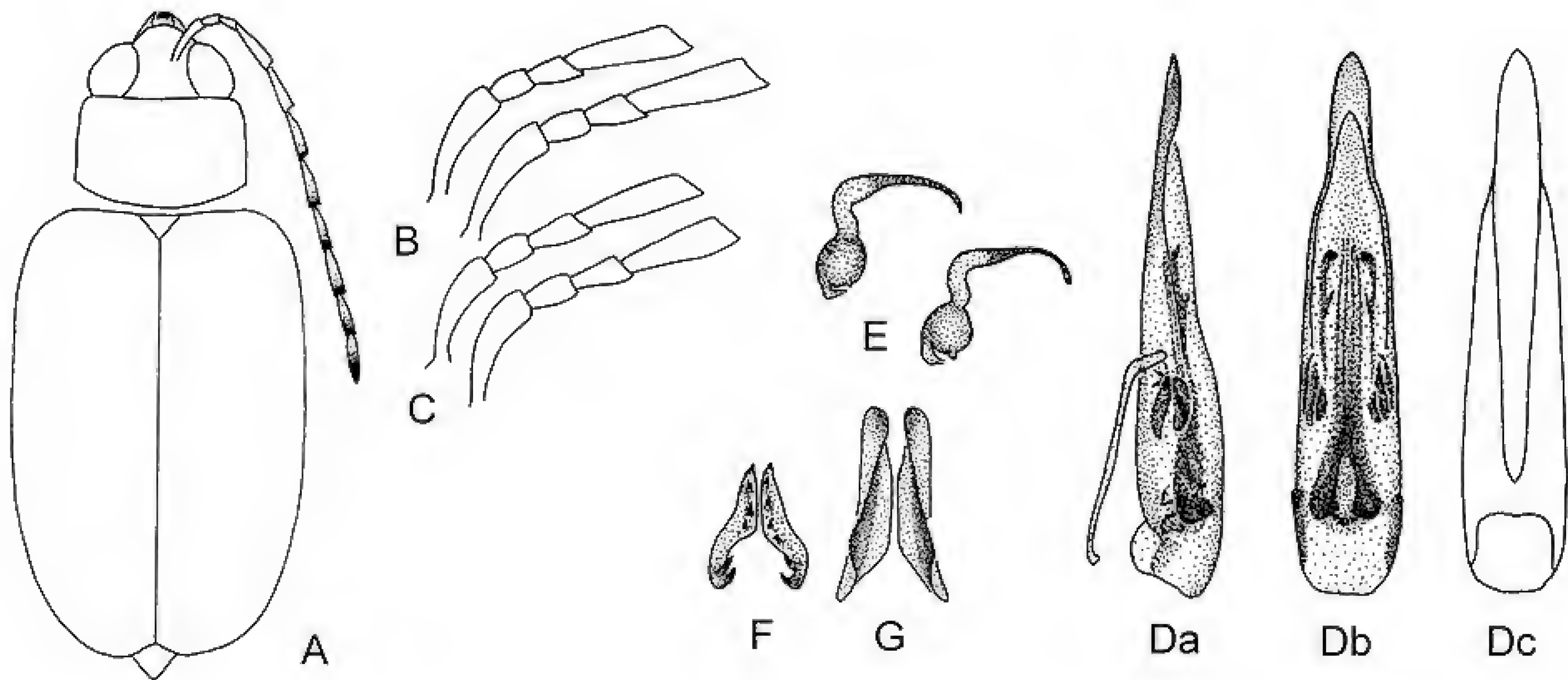


Fig. 18. *Monolepta citrinella* Jacoby, 1899. **A.** Colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

Diagnosis. *Monolepta citrinella* is characterized by its entirely yellow coloration. Some specimens are pale yellow, rarely whitish. It is the only species with this coloration in North-East Africa. Other species with entire yellow dorsum like *M. livingstoni* (Jacoby, 1900), *M. pimenteli* Laboissière, 1939, and *M. hiebei* Wagner, 2016 are all restricted to southern Africa.

Distribution and ecology. Widely distributed in savannahs and semi-deserts up to desert biomes in tropical Africa (Fig. 10). This almost pan-afrotropical distribution has resulted in a large number of synonyms. Many specimens were collected by light trapping (some of them in moth traps, and then completely covered by lepidopteran scales). The absence of an aposematic pattern and large eyes are also typical characters of nocturnal beetles.

Monolepta leuce Weise, 1903

(Figs 4, 19)

Monolepta leuce Weise, 1903: 214.

= *Monolepta puncticeps* var. A. Chapuis, 1879: 24.

Further material examined. 49 specimens, 17 findings. **Eritrea.** 7 ex., Umg. Asmara, 15.20N/39.00E, VII.2001, L. & M. Stalmans (IRSN). – **Ethiopia.** 15 ex., Alemaya, 9.24N/42.01E, Bob Hill, Celtis Africana, VI.1964 (USNM); 1 ex., Wolisso, Ghion, 8.32N/37.58E, VI.1965, A. B. Gurney (USNM); 5 ex., Rock Valley nr. Harar, VI.1965, A. B. Gurney (USNM); 5 ex., Alemaya, VI.1965, A. B. Gurney (USNM); 2 ex., Jimma, 7.40N/36.50E, VII.1965, A. B. Gurney (USNM); 3 ex., Addis, IV.1971, B. Feinstein (USNM). – **Kenya.** 1 ex.,

Lombwua, 0.02S/37.35E, Sandb. (NHRS); 1 ex., Mt. Elgon, V. Clausnitzer (ZFMK); 1 ex., 30 min., NW Nairobi, I.1968, K. V. Krombein (USNH); 1 ex., Nyeri, 0.25S/36.57E, II.1968, P. J. Spangler (USNM); 1 ex., Gatamayu, 0.58S/36.42E, 2330 m, II.1999, Th. Wagner (ZMFK); 1 ex., L. Naivasha, 0.23S/36.26E, sweeping Lake margin, X.2005 (CDr). – **Tanzania.** 1 ex., Ngorongoro, 3.11S/35.34E, VIII.1978, G. Scudder (BMNH); 1 ex., Segera Camp am Highway Hotel, 5.19S/38.33E, 325 m, 23.II.2008, U Heinig (CHe); 1 ex., Gonja, Chome NR, Soth Pare Mts., 4.15S/37.58E, XII.2011, Smith & Takano (BMNH); 2 ex., Mt. Meru NP, 3.14S/36.50E, IV.2012, Smith & Takano (BMNH).

Remarks. A detailed redescription was published in Wagner (2007b) that based on 755 studied specimens. Next to the female lectotype from Tanzania “Type / Mombo 7.99 / *Monolepta leuce* m. / ex. coll. J. Weise” (MNHB), a „variation type“ of *Monolepta puncticeps* var. A., a species synonymised with *M. cruciata* Guérin de Méneville, 1847 was described from Ethiopia “Abyss. Raffray / *Monolepta puncticeps* Chap. Type var.”. The younger name *M. leuce* has priority since the older name is infra-subspecific and thus not available, because a single letter as species name is not conform with the ICZN rules (cf. 11.9.1.).

Diagnosis. Most similar to *M. pauperata* which occurs allopatrically in lowland areas of Western Africa and can be easily distinguished by completely yellowish-red underside and the distinct elytral coloration. *Monolepta deleta* that is sympatric in Kenyan and Tanzanian High-

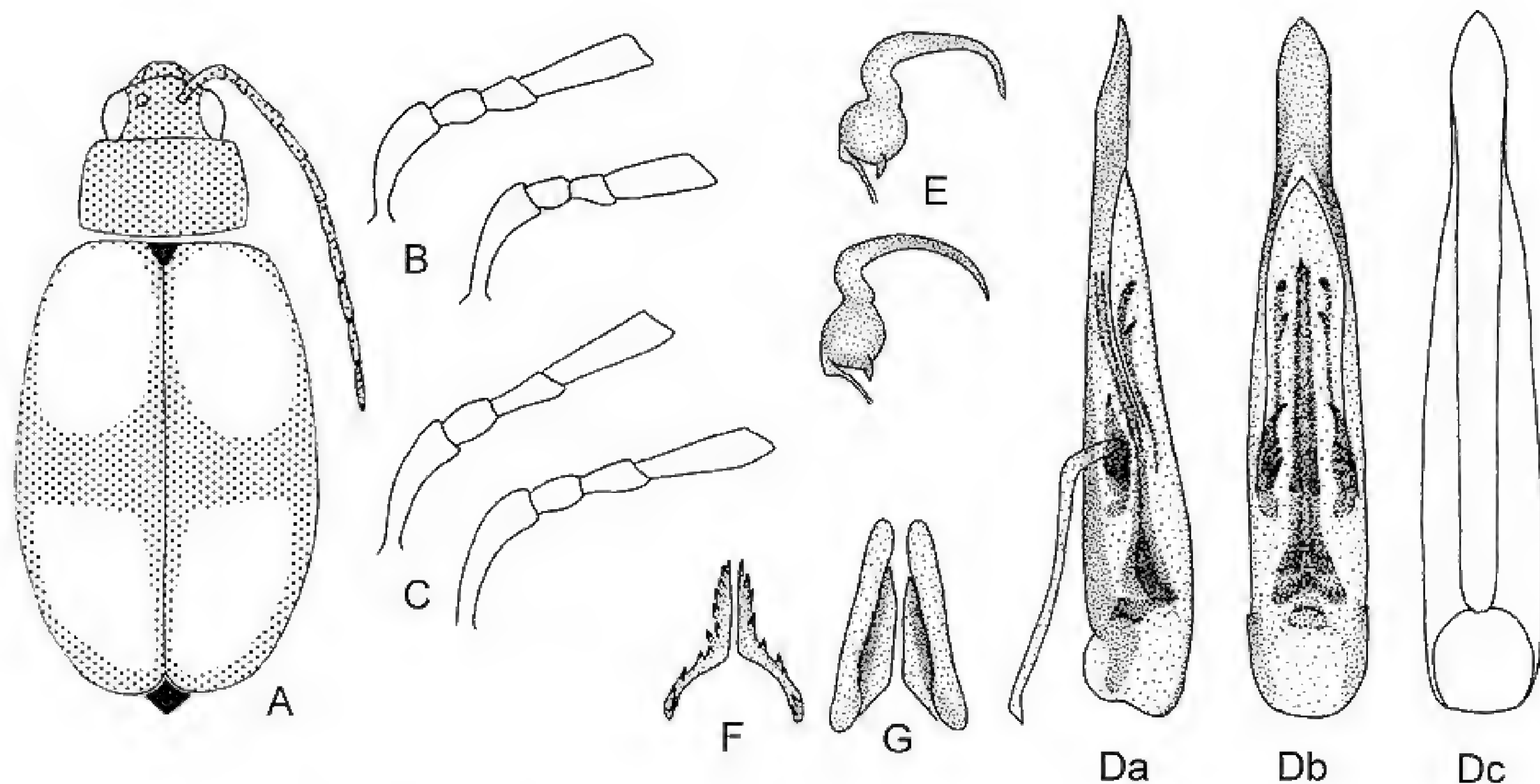


Fig. 19. *Monolepta leuce* Weise, 1903. **A.** Colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

lands, is on average smaller, elytra are broader and the pronotum is narrower and more bulged than in *M. leuce*. Most evident are the complete black antenna and legs of *M. deleta*. There are very few *M. cruciata* with pale elytral coloration similar to *M. leuce* (Figs 13Ad, 19A), but there is at least at black spot at humerus and black subhumeral margins.

Distribution and ecology. An abundant species of predominantly montane areas along the East African Rift from Eritrea through Ethiopia, Kenya, Tanzania southwards to Lake Malawi (Fig. 4).

***Monolepta jeanneli* Laboissière, 1920**

(Figs 2, 20)

Monolepta jeanneli Laboissière, 1920: 51.

= *Monolepta burgeoni* Laboissière, 1940: 71; Wagner 2000: 230.

= *Monolepta seminigra* Bryant, 1953: 868; Wagner 2000: 230.

= *Monolepta pallipes* Bryant, 1953: 867; Wagner 2000: 230.

= *Monolepta kiwuensis* Weise, 1924; syn. nov.

Type material. New synonymy: *Monolepta kiwuensis* Weise, 1924: Holotype, female, „Ituru omrâd. / Kivu sjön / *Monolepta kiwuensis* m. / Holotypus *Monolepta kiwuensis* Weise, 1924 / *Monolepta jeanneli* Laboissière, 1920 Th. Wagner det.“ (NHRS). Holotype by indication in the original publication „Kivu See, 1 ♀“.

Further material examined. 26 specimens, 19 findings.

Congo (Democratic Republic). 1 ex., Parc Nat. Garamba, Mt. Tungu, VI.1952, Miss. H. de Saeger (MRAC); 1 ex., Parc Nat. Albert, Munagana, 1.18S/29.36E, VIII.1934, G. F. de Witte (IRSN). – **Ethiopia.** 2 ex., Lake Shola, 170 km S of Addis Abeba, 7.40N/38.40E, XI.1990, Fabaceae, L. Medvedev (CME). – **Kenya.** 1 ex., Chyulu Hills, 2.35S/37.50E, V.1976, ca. 1500 m, J. Kriken (NNML); 1 ex., Mt. Elgon, Kaptega, 1.16N/34.52E, 1980 m, I.1979, T.-E. Leiler (NHRS); 1 ex., Nairobi, 1.17S/36.50E, II.1979, T.-E. Leiler (NHRS); 2 ex., Mt. Elgon, nr. Chepnyalli Cave, dry evergreen montane forest, 2500 m, no. 509, at light, I.1992, O. Merkl & G. Várkonyi (HNHM); 3 ex., Hells Gate NP, 0.56S/36.19E, Tarchonanthus, IV.1998 (CDr); 2 ex., Ol-Njoroma Gorge, Hells Gate, IV.1997 (CDr); 1 ex., Hells Gate NP, sweeping Lake margin, X.2005 (CDr). – **Tanzania.** 1 ex., Morogoro, 6.59S/37.40E, 580 m, light trap, III.–IV.1987, Pócs & Sontera (HNHM); 1 ex., Seronera, XII.1995, lumière, ex. coll. J. Roggeman (CBe); 1 ex., Tanz., 1250 m, 3°50S/30.42E, pr. Igoma, XII.2006, F. Kantner (CKa); 1 ex., Ngorongoro, Sima camp, 2319 m, 3.13S/35.29E., IV.2012, Light trap, Smith & Takano (BMNH); 1 ex., Kilimamoja, Kibaone, 3.23S/35.49E, IV.2012, Light trap, Smith & Takano (BMNH). – **Uganda.** 1 ex., 0.19N/32.35E, Kampala (ZMUH); 1 ex., Kibale Forest, 0.50N/31.06E, Sweep pine, IV.1984, M. Nummelin (MZHF); 1 ex., Budongo F., near Sonso river, 1.45N/31.35E, Th. Wagner (ZFMK); 2 ex., SE of Hoima, XI.2001, Snizek (NME).

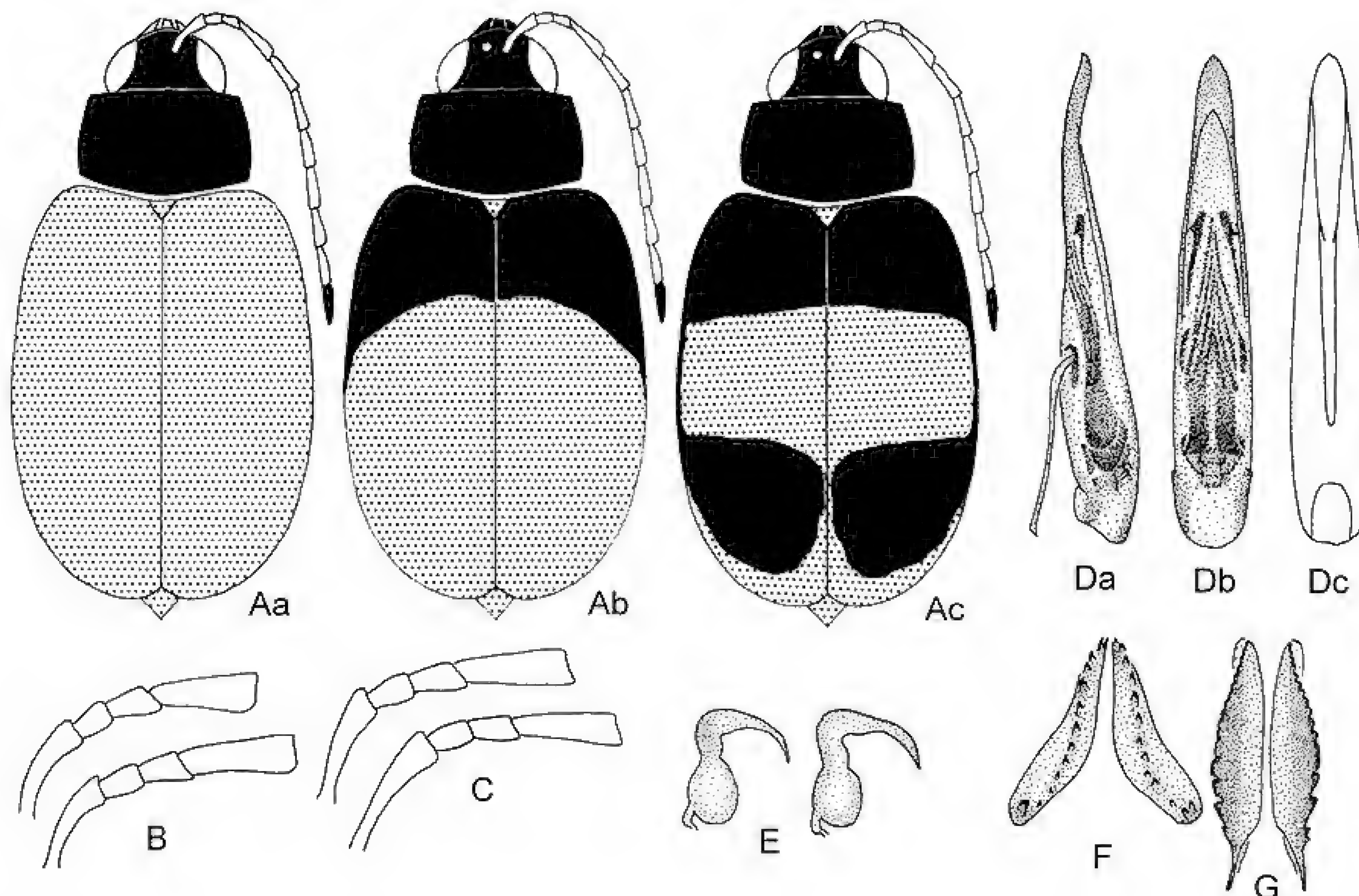


Fig. 20. *Monolepta jeanneli* Laboissière, 1920. **A.** Three different colour patterns. **B.** Basal antennomeres, males. **C.** Dto., females. **D.** Median lobe, a. lateral, b. dorsal, c. ventral, without endophallic structures. **E.** Spermathecae. **F.** Bursa-sclerite, dorsal. **G.** Dto., ventral.

Remarks. A detailed redescription was published in Wagner (2000), based on 175 specimens out of 93 findings. The type material of the valid name originate from the Kikuyu Escarpment in Central Kenya.

Diagnosis. Characterized by large, broad size, red elytral coloration, pale yellow legs and antennae. In Ethiopia and Eritrea the only *Monolepta* species with predominantly red dorsal coloration.

Distribution. Quite common in Central and East Africa from lowland to montane regions, very rare in northeast Africa (Fig. 2).

IDENTIFICATION KEY

The following key can be used for all specimens of “true” *Monolepta* from North-East Africa, including the states Egypt, Sudan, South-Sudan, Ethiopia, Eritrea, Djibouti and Somalia. Up to now, 15 species of *Monolepta* are known from this region, seven of them endemic to the area, mainly from the Ethiopian Highlands.

- 1 Upperside completely yellow; basal antennomeres very slender (Fig. 18B, C); total length 4.0–5.2 mm. Widely distributed in the Afrotropical Region, rarely found in North-East Africa (Fig. 10). – N.B: Several species of galerucines with elongated basimetatarsus, possessing an entirely yellow coloration are known from Africa, some of them originally described in *Monolepta*, but do not belong to this group. Allocation to the genus should be confirmed by genital dissection in doubtful cases.....*M. citrinella* Jacoby, 1899
- Elytra carmine red, yellow with reddish outer margins, or yellow with black markings..... 2
- 2 Elytra entirely carmine red (Fig. 20Aa), often with broad black base (Fig. 20Ab), rarely with additional black band in the apical third (Fig. 20Ac); large and broad species, total length 4.50–5.10 mm; ratio length of elytron to maximal width of both elytra 0.72–0.76. Mainly in wet tropical forests of Central and East Africa, rarely found in the Ethiopian Highlands (Fig. 2)*M. jeanneli* Laboissière, 1920
- Elytra yellow, with black markings (e.g. Figs 1A, 5A, 9A, 15A), sometimes with red suture (Figs 13Ab,

- 16A), or with completely red outer margins (Figs 13Ad, 19A) 3
- 3 Elytra black at base, usually as broad band, and one further transverse black band, rarely reduced to a smaller spot (Fig. 15Aa, Ac), in the apical third of elytra; elytral outer margins and apex not black (Figs 14A, 15A) 4
- Elytra yellow, with black markings (e.g. Figs 1A, 5A, 9A), with or without transverse black band in the middle, and usually with black elytral tip and outer margins, sometimes with red suture (Figs 13Ab, 16A), or with completely red outer margins (Figs 13Ad, 19A) 5
- 4 Third antennomere significantly longer than second, length of second to third antennomere 0.75–0.88 (Fig. 14B–C), and about half as long as fourth antennomere, length of third to fourth antennomere 0.46–0.54; pronotum comparatively slender, pronotal length to width 0.63–0.67; larger, total length 3.8–5.3 mm; apex of median lobe slightly spoon-like enlarged (Fig. 14D). Abundant in coastal regions of North-East Africa, the Near East and the Arabian Peninsula (Fig. 7) *M. lepida* Reiche, 1858
- Third antennomere shorter, roughly of same length as second, length of second to third antennomere 0.86–1.00, length of third to fourth antennomere 0.28–0.37 (Fig. 15B–C); pronotum broader, pronotal length to width 0.58–0.65; on average smaller, total length 3.2–4.7 mm; apex of median lobe more slender, parallel-sided (Fig. 15D–F.); most specimens from North-East Africa like coloration type Fig. 15Ae. Abundant species throughout tropical Africa with exception of the South (Fig. 7) *M. vincta* Gerstaecker, 1871
- 5 Elytra with completely red outer margins (Figs 13Ad, 19A) 6
- Elytra at least with significant black base (e.g. Figs 1A, 6A, 17A), rarely with narrow black outer margins and suture (Figs 9Aa, 11Aa) 7
- 6 Dorsum reddish to reddish-brown, elytra with yellow ovate spots in the basal and apical half, separated by a reddish transverse band (Fig. 19A); underside and scutellum contrasting black; total length 3.7–5.3 mm. Restricted to and abundant in the East African Rift and adjacent areas, predominantly montane zones from Eritrea and Ethiopia through Kenya and Tanzania towards Lake Malawi (Fig. 4) .
..... *M. leuce* Weise, 1903
- At least with black humeral tip; scutellum and underside yellow (Fig. 13Ad); rare coloration (see duplett 8) *M. cruciata* Guérin de Méneville, 1849
- 7 Elytra with entirely (Fig. 16Aa, Ac) or partly red suture (Figs 5A, 13Ab, 16Ab) 8
- Elytra only yellow with dark brown to black markings 10
- 8 Large, total length 4.3–7.1 mm; usually with three black transverse bands and entirely red suture (Fig. 16Aa, Ac), or at least subscutellar red sutural stripe and red scutellum (Fig. 5A, 16Ab); basal antennomeres slender (Figs 5B–C; 16B–C); median lobe broad lanceolate at apex (Figs 5D, 16D), spermatheca with large spherical nodulus (Figs 5E, 16E) 9
- Smaller, total length 4.1–5.2 mm; cross-like elytral pattern with narrow black or partly red outer margins and suture, if suture partly red, subscutellar base black (Fig. 13Ab); basal antennomeres broader, in particular in males (Fig. 13B); median lobe narrowed and slender at apex (Fig. 13D–E), spermatheca with smaller spherical nodulus (Fig. 13F). With exception of the West, one of the most abundant *Monolepta* species in Africa, also frequently found in Ethiopia (Fig. 2) *M. cruciata* Guérin de Méneville, 1849
- 9 Elytra with broad transverse black band, only narrow red along the basal part of suture and at elytral tip, no red along outer suture (Fig. 5A); median lobe more slender, ventral groove narrow, lateral endophallic spiculae have a small apical enlargement (Fig. 5D); rare endemic species of the Ethiopian Highlands (Fig. 2) *M. euchroma* Fairmaire, 1883
- Elytral transverse bands usually narrower, suture entirely red (Fig. 16Aa, Ac) and/or outer elytral margins partly red (Fig. 16Aa–Ac); median lobe broader, ventral groove broader in the middle, lateral endophallic spiculae with hammer-like enlargement (Fig. 16D); widely distributed and abundant throughout the Afrotropical Region (Fig. 12)
..... *M. vinosa* Gerstaecker, 1871
- 10 Elytra with entirely black outer margins and suture, without (Figs 9Aa, 9Ab, 11Aa), or with median transverse band, given a cross-like pattern (Figs 8A, 9Ac, 9Ad, 11Ab, 13Aa, 13Ac) 11
- Elytra not entirely black at margins, usually only in the basal half, without median transverse band and cross-like pattern (Figs 1A, 3 A, 6A, 17A) 16
- 11 Pronotum red with significant black margins (Fig. 8A); large, 5.20–5.60 mm; median lobe very broad (Fig. 8D); restricted to Eritrea, Ethiopia and Sudan (Fig. 7)
..... *M. marginethoracica* Laboissière, 1940
- Pronotum yellow to reddish-yellow, without black margins, or entirely black; smaller, 3.90–5.20 mm; median lobe of other type 12

- 12** Elytra with black suture and margins only, without transverse band (Figs 9Aa, 9Ab, 11Aa) **13**
- Elytra with cross-like pattern due to four yellow spots (Figs 9Ac, 9Ad, 11Ab, 13Aa, 13Ac) **14**
- 13** Pronotum broad, pronotal length to width 0.57–0.63 (Fig. 9A), yellow or black; total length at least 3.9 mm, apex of median lobe very slender, parallel-sided (Fig. 9D); abundant and endemic in the Ethiopian Highlands (Fig. 10)..... ***M. nigrocruciata* Laboissière, 1940**
- Pronotum more slender, pronotal length to width 0.62–0.67 (Fig. 11A), black; smaller, total length 3.5–4.7 mm, apex of median lobe broad, spoon-like (Fig. 11D); abundant and endemic in the Ethiopian Highlands (Fig. 12) .. ***M. gobensis* Laboissière, 1940**
- 14** Elytra relatively broad, width of both elytra to length of elytron 0.66–0.74; apical part of median lobe slender, conical (Fig. 13D–E); head and pronotum usually yellow (Fig. 13Ac), if pronotum red, at least base yellow (Fig. 13Aa, Ab) (see duplett 8).....
- ***M. cruciata* Guérin de Méneville, 1849**
- Elytra more slender, width of both elytra to length of elytron 0.62–0.70; apical part of median lobe slender, but more parallel-sided (Fig. 9D) or broad at apex (Fig. 11D); head and pronotum entirely red (Fig. 9Aa–9Ac) or black (Figs 9Ad, 11Ab) **15**
- 15** Apex of median lobe very slender, parallel-sided (Fig. 9D) (see duplett 13).....
- ***M. nigrocruciata* Laboissière, 1940**
- Apex of median lobe broad, spoon-like (Fig. 11D) (see duplett 13)..... ***M. gobensis* Laboissière, 1940**
- 16** Elytra with broad black base, triangularly enlarged along suture (Fig. 3A); large 4.8–5.6 mm; median lobe broad conical towards apex (Fig. 3D); very abundant endemic in the Ethiopian Highlands (Fig. 4)..... ***Monolepta postrema* Chapuis, 1879**
- Elytra narrow black at base (Figs 1A, 3A, 16A); usually smaller 3.6–5.4 mm; median lobe different..
- **17**
- 17** Elytra with saddle-like black coloration (Fig. 17A); small, total length: 3.6–4.8 mm; median lobe dorso-ventrally compressed, conical, pointed at apex (Fig. 17D); restricted to montane areas of Ethiopia, Uganda, Kenya, Rwanda and northern Tanzania (Fig. 12)..... ***M. ephippiata* Gerstaecker, 1871**
- Basal half of elytra with narrow black base and margin, along suture somewhat enlarged towards the middle (Figs 1A, 6A); same size or larger; median lobe enlarged at apex (Figs 1D, 6D) **18**

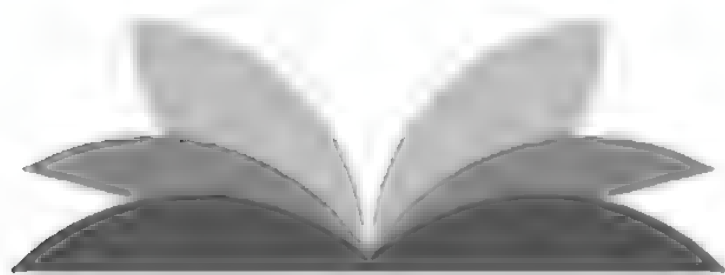
- 18** Smaller, 4.0–4.8 mm; elytra more slender, width of both elytra to length of elytron 0.62–0.70; pronotum red (Fig. 1A); median lobe slender, lateral spiculae twisted (Fig. 1D); rare endemic species of the Ethiopian Highlands (Fig. 2).....
- ***Monolepta longiuscula* Chapuis, 1879**
- Larger, 4.6–5.4 mm; elytra slightly broader, width of both elytra to length of elytron 0.62–0.68; pronotum yellow (Fig. 6A); median lobe broader, lateral spiculae straight (Fig. 6D); rare endemic species of the Ethiopian Highlands (Fig. 2).....
- ***Monolepta nigropicta* Laboissière, 1938**

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The Coccinellidae (Coleoptera) from El Hierro, Canary Islands

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⁴[urn:lsid:zoobank.org:author:ADA36F13-ECF6-4B09-B6B7-2E96CA945E0F](https://zoobank.org/author:ADA36F13-ECF6-4B09-B6B7-2E96CA945E0F)

⁵[urn:lsid:zoobank.org:author:D741C759-6CDD-4B61-BE93-3ECC2918A73F](https://zoobank.org/author:D741C759-6CDD-4B61-BE93-3ECC2918A73F)

Abstract. In this study, Coccinellidae were collected and observed at 42 sites located on El Hierro (Spain), the westernmost island of the Canary archipelago, during 2017 and 2019 excursions. A total of 1553 specimens belonging to 18 species were recorded, of which four species are newly reported from El Hierro. The total number of ladybird species so far documented to inhabit El Hierro is 22. After examination of the morphological features *Scymnus cercyonides* Wollaston, 1864 is transferred from the subgenus *Pullus* Mulsant, 1846 to *Mimopullus* Fürsch, 1987. *Chilocorus canariensis* Crotch, 1874 and *Novius canariensis* Korschefsky, 1935 are confirmed to be valid species.

Key words. Spain, West Palaearctic, ladybird beetles, new records, endemic species.

INTRODUCTION

The Canary Islands are situated in the northeast Atlantic Ocean near the African coast and belong to the Mediterranean Basin biodiversity hotspot (Myers et al. 2000). They have a subtropical climate strongly influenced by the humid trade winds, with temperatures showing little seasonal variation: mean temperature in winter is 18 °C and in summer 24 °C (Juan et al. 2000; Espadaler 2007). The fauna of the Canary Islands is characterized by a high level of endemism. For example, among the Canarian invertebrates endemism is estimated at about 50% (Juan et al. 2000).

The fauna of Coccinellidae of the Canary Islands has a long history of exploration pioneered by Wollaston (1864) and summarized by Eizaguirre (2007) and Oromí et al. (2010). More than 50 species of ladybird beetles were reported from the archipelago. The highest numbers of species were reported from Gran Canaria (42) and Tenerife (41) (Eizaguirre 2007; Oromí et al. 2010; Suarez et al. 2018, Romanowski et al. 2020a), large islands, well-known for their concentration of endemic diversity (Reyes-Betancort et al. 2008). However, Coccinellidae were not deeply investigated on all islands of the archipelago, and only 18 species have so far been reported from El Hierro (Franz 1995; Oromí et al. 2010). Recent study by Romanowski et al. (2018, 2019) nearly doubled

number of ladybird species reported from Fuerteventura and indicated that this eastern island of the Canary archipelago was less prospected than central islands such as Tenerife and Gran Canaria. This study aims to provide new information on species richness of ladybird beetles of El Hierro.

MATERIAL AND METHODS

El Hierro is the westernmost and also the smallest (269 km²) and geologically youngest island of the Canary archipelago, formed by volcanic eruptions approximately 1.1 million years ago (Fernández-Palacios & Whittaker 2008). A wide range of natural habitats can be found on the island (Fig. 1) along with decorative plants sustained by irrigation that grow in parks, hotel grounds and gardens. Due to a well-preserved biological diversity, since 2000 El Hierro has the status of a biosphere reserve.

Coccinellidae were collected and observed at 42 sites on El Hierro between 28 January and 2 February 2017 and between 6 and 12 April 2019. Study sites were located along the coast and inland of the island (Table 1). The beetles were mostly shaken down from various trees and shrubs on a 1 m × 1 m white beating sheet and were swept from ground cover with a net. Some ladybirds were picked from vegetation after direct observation.

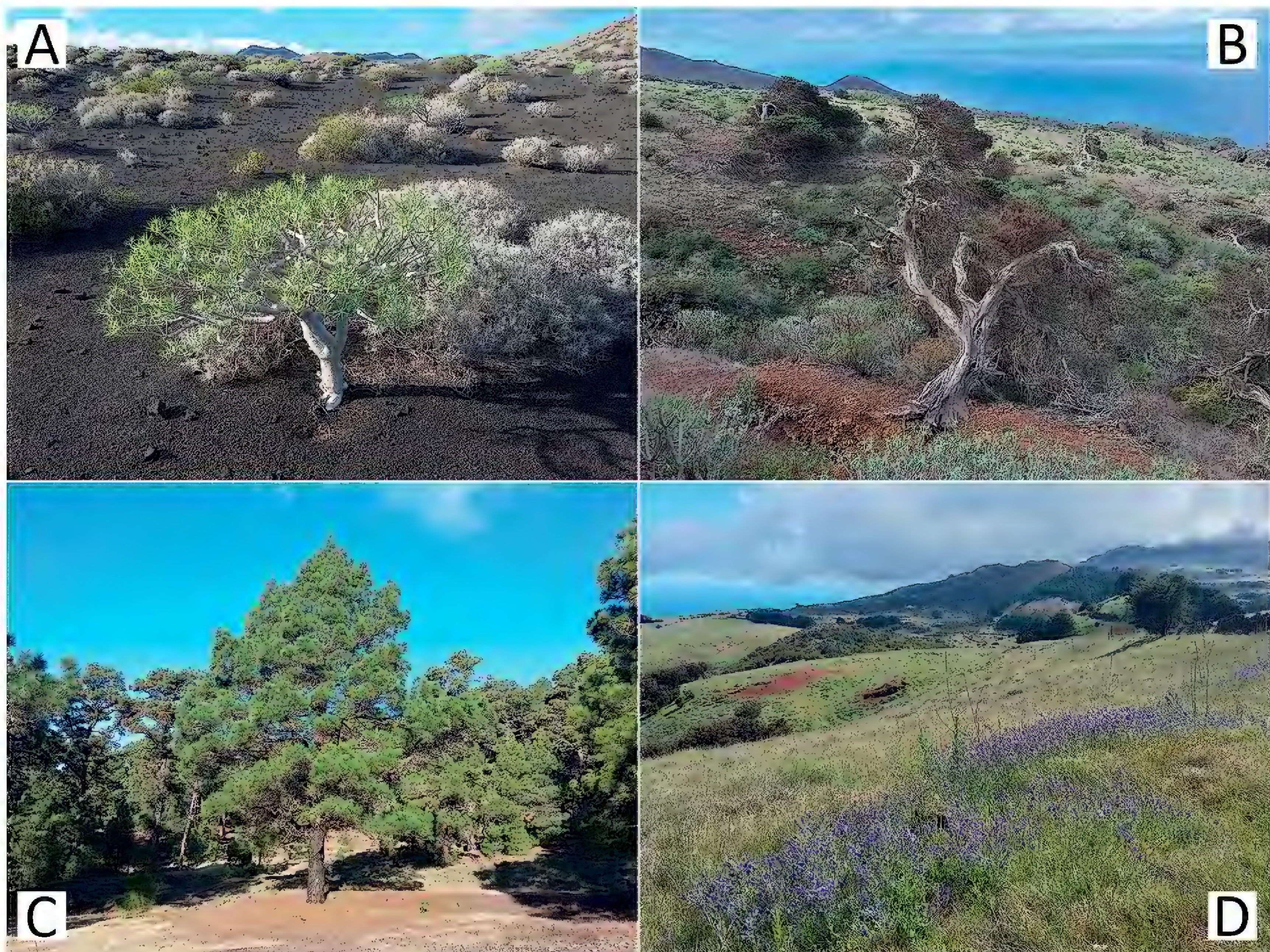


Fig. 1. Habitats surveyed for ladybird beetles on El Hierro. **A.** Halophile vegetation. **B.** Junipers *Juniperus* sp. in Sabinar. **C.** Pine forest. **D.** Agricultural land.

The voucher specimens collected by J. Romanowski and C. Zmuda are stored in the insect collection at the Institute of Biological Sciences, Cardinal Stefan Wyszyński University in Warsaw and those collected by J. Krátký and J. Pelikán are deposited in private collection of Jaroslav Větrovec.

The nomenclature of ladybird beetles, unless specifically discussed, follows Kovář (2007), and systematic arrangement follows Ślipiński (2007) and Seago et al. (2011). List of synonyms is provided only for species which were not mentioned in the previous works (Romanowski et al. 2019; Romanowski et al. 2020b).

RESULTS

During the research, a total of 1553 Coccinellidae specimens (1545 imagines, 3 pupae, and 5 larvae) belonging to 18 species were recorded, of which four are new to El Hierro. Below, the data on the recorded species are provided together with supplementary photographic infor-

mation on the identification of several species of special interest.

List of taxa found on El Hierro during this study

Coccinellinae Latreille, 1807

Chilocorini Mulsant, 1846

Chilocorus canariensis Crotch, 1874

Fig. 2A–F

Material examined. Valverde (30.I.2017), 1 ex. (leg. J. Krátký); Las Puntas (29.I.2017), 2 exx. (leg. J. Krátký); El Chirgo (29.I.2017), 1 ex. (leg. J. Pelikán); Tamaduste (30.I.2017), 1 ex. (leg. J. Krátký); Árbol Garoé, Echedo, El Juan, El Mocanal, Guarazoca, Hoya del Morcillo, La Caleta, La Dehesa, Las Playas, Mirador de Isora, Montaña de la Casilla, Pozo de las Calcosas, Punto de la Dehesa, Sabinar, Tigaday, Valverde (6–12.IV.2019), total of 57 exx. (55 adults, 2 larvae) collected from various

Table 1. Collecting sites of ladybird beetles on El Hierro.

No.	Location	Coordinates
1	Árbol Garoé	27°47'22"N 17°56'35"W
2	Camino de Jinama	27°45'12"N 17°59'28"W
3	Charco Menso	27°50'52"N 17°55'24"W
4	Cueva de Don Juste	27°38'54"N 17°59'31"W
5	Echedo	27°50'03"N 17°55'22"W
6	El Chirgo	27°45'04"N 18°03'06"W
7	El Greeting	27°44'22"N 18°04'56"W
8	El Juan	27°42'46"N 18°02'53"W
9	El Mocanal	27°49'14"N 17°56'41"W
10	El Pinar	27°41'43"N 17°58'35"W
11	El Sabinal	27°43'48"N 18°07'14"W
12	El Tiñor	27°47'21"N 17°56'03"W
13	El Tomillar	27°43'28"N 18°06'23"W
14	Eremita de San Salvador	27°43'56"N 18°00'37"W
15	Guarazoca	27°48'35"N 17°58'24"W
16	Hoya del Morcillo	27°42'51"N 17°59'49"W
17	Isora	27°45'09"N 17°56'51"W
18	La Caleta	27°48'03"N 17°53'14"W
19	La Dehesa	27°43'47"N 18°08'30"W
20	La Restinga	27°38'29"N 17°58'55"W
21	Las Playas	27°43'04"N 17°57'31"W
22	Las Puntas	27°47'31"N 17°59'29"W
23	Malpaso	27°43'43"N 18°02'26"W
24	Mirador de Isora	27°44'19"N 17°57'04"W
25	Mirador de Jinama	27°45'46"N 17°58'50"W
26	Mirador de las Playas	27°43'57"N 17°58'22"W
27	Montaña de Cascaja	27°47'24"N 17°58'21"W
28	Montaña de la Casilla	27°43'15"N 17°58'50"W
29	Montaña de Masilva	27°43'51"N 17°59'31"W
30	Montaña de Mercadel	27°42'39"N 18°01'17"W
31	Montaña del Gajo	27°43'44"N 17°59'29"W
32	Montaña del Lajura	27°40'41"N 17°58'48"W
33	Pista del Derrabado	27°44'27"N 18°03'51"W
34	Pozo de la Salud	27°45'22"N 18°06'14"W
35	Pozo de las Calcosas	27°50'23"N 17°56'48"W
36	Punto de la Dehesa	27°45'59"N 18°07'48"W
37	Sabinar	27°44'55"N 18°07'37"W
38	Sabinosa	27°44'51"N 18°05'51"W
39	San Andres	27°46'06"N 17°57'53"W
40	Tamaduste	27°49'30"N 17°53'44"W
41	Tigaday	27°45'06"N 18°01'36"W
42	Valverde	27°48'38"N 17°54'52"W

plants, including *Yucca* sp., *Euphorbia* sp., *Juniperus* sp., *Nerium oleander* L. (leg. J. Romanowski and C. Zmuda).

Distribution. Endemic Canarian species.

Remarks. Wollaston (1864) examined specimens of this species from the Canary Islands and stated that they belong to the common European species *Ch. renipustulatus* (Scriba, 1790). However, Crotch (1874) in his revision of the ladybird beetles of the world, recognized it as a separate species. Since that time various authors treated it as a subspecies of *Ch. renipustulatus* (Franz 1995; Eizaguirre 2007; Nicolas 2010; Nicolas & Rae 2012) or as a distinct species (Kovář 2007; Hernández et al. 2009). To confirm the status of the Canarian specimens we compared the genitalia of both sexes with those of *Ch. renipustulatus* collected in Poland (Fig. 2G–K). Without a doubt, *Ch. canariensis* should be treated as a distinct, endemic Canarian species, and *Ch. renipustulatus* should be excluded from the list of ladybird beetles of the Canary Islands.

Differential diagnosis. *Chilocorus canariensis* can be separated externally from *Ch. renipustulatus* by the shape of red maculae on elytra (Fig. 2A). In *Ch. canariensis* elytral maculae form a transverse band in the central part of each elytron, while in *Ch. renipustulatus* maculae are almost rounded with a regular border. Differences in male genitalia: in *Ch. canariensis* penis guide asymmetrical (Fig. 2D–E), about as long as parameres, parameres shortly setose, apex of penis with screw-shaped carina with more dense coils (Fig. 2F); in *Ch. renipustulatus* penis guide symmetrical (Fig. 2I–J), distinctly shorter than parameres, parameres with longer setae, apex of penis with screw-shaped carina more loose (Fig. 2K). Differences in female genitalia: in *Ch. canariensis* (Fig. 2C) spermatheca with apical projection more sclerotized and twice longer than in *Ch. renipustulatus* (Fig. 2H).

***Parexochomus nigripennis* (Erichson, 1843)**

Material examined. Las Puntas (29.I.2017), 1 ex. (leg. J. Krátký).

Distribution. Reported from all islands of the Canary archipelago excluding La Palma (Eizaguirre 2007; Oromí et al. 2010). Outside of the Canary Islands known from Algeria, Egypt, Libya, Tunisia, Morocco, Iran, Italy, Portugal, Spain, Saudi Arabia, United Arab Emirates, Iran, Pakistan and India (Poorani 2002; Kovář 2007; Biranvand et al. 2017; Abied et al. 2018; Lakhal et al. 2018).

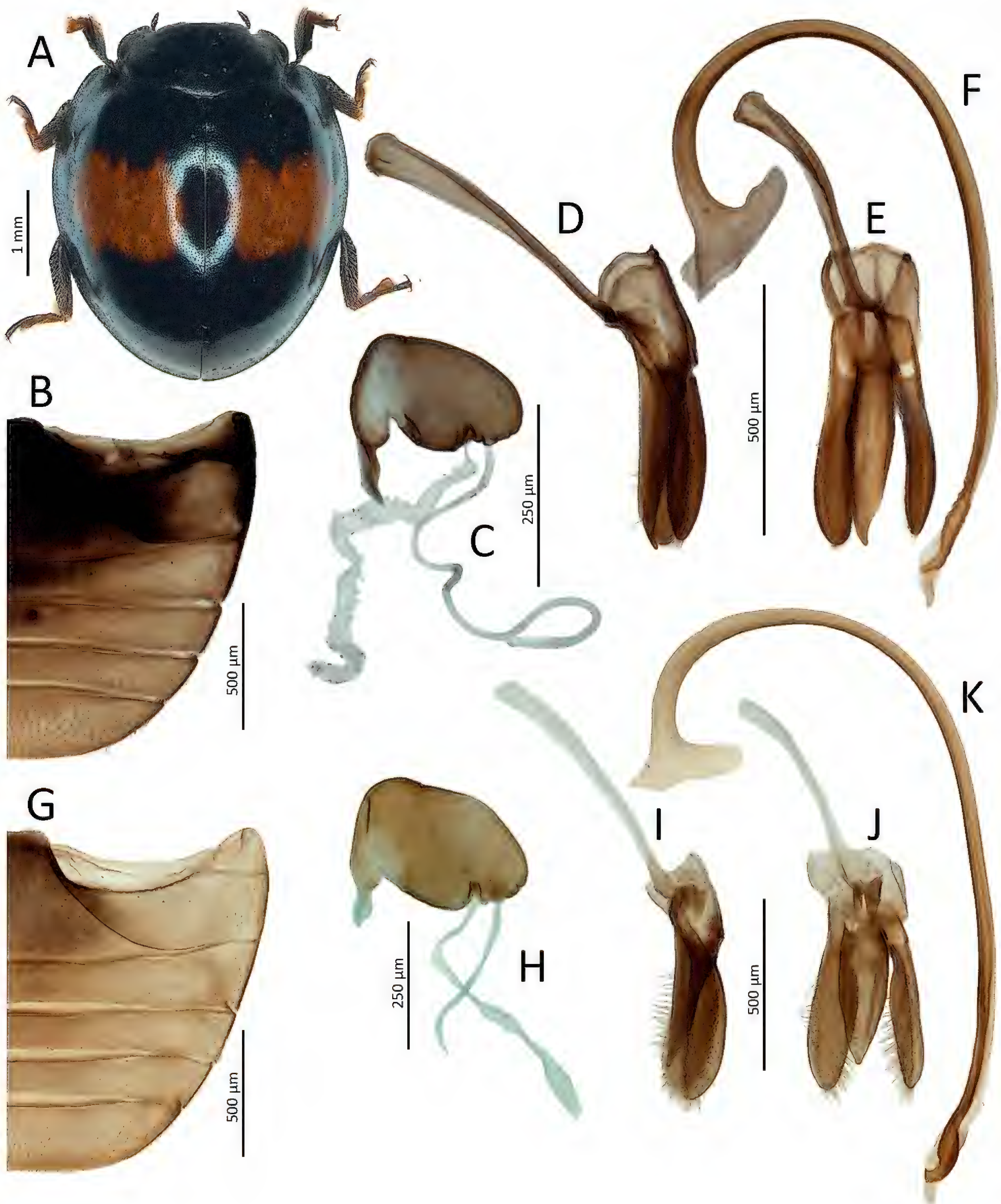


Fig. 2. A–F. *Chilocorus canariensis* Wollaston. A. Habitus. B. Abdomen, male. C. Spermatheca, spermduct and accessory gland. D. Tegmen, lateral. E. Tegmen, inner. F. Penis, lateral. G–K. *Chilocorus renipustulatus* (Scriba). G. Abdomen, male. H. Spermatheca, spermduct and accessory gland. I. Tegmen, lateral. J. Tegmen, inner. K. Penis, lateral.

Coccidulini Mulsant, 1846***Cryptolaemus montrouzieri* Mulsant, 1853**

Material examined. Echedo (12.IV.2019), 1 ex. on *N. oleander*; Tamaduste (11.IV.2019), 1 ex. on *Bougainvillea* sp. (leg. J. Romanowski and C. Zmuda).

Distribution. An Australian species spread throughout the world (Kairo et al. 2013). Reported from all Canary Islands (Eizaguirre 2007; Oromí et al. 2010; Romanowski et al. 2019, 2020b).

***Nephus flavopictus* (Wollaston, 1854)**

Fig. 3G

Material examined. Pozo de la Salud (28.I.2017), 1 ex. (leg. J. Krátký); El Pinar (31.I.2017), 1 ex. (leg. J. Pelikán) from *Euphorbia* sp.; El Tiñor (1.II.2017), 1 ex. (leg. J. Pelikán); Pozo de las Calcosas, Charco Menso, Cueva de Don Juste, El Mocanal, El Tomillar. Guarazoca, Isora, La Caleta, La Restinga, Pozo de la Salud, Sabinar, Tamaduste, Tigaday, Valverde (7–12.IV.2019), total of 96 exx. collected from various plants, including *Euphorbia* sp., *Juniperus* sp., *Yucca* sp., *N. oleander*, *Pistacia lentiscus* L. and *Bougainvillea* sp. (leg. J. Romanowski and C. Zmuda).

Distribution. Endemic Macaronesian species, reported from the Canary Islands (Fürsch 1987; Eizaguirre 2007; Oromí et al. 2010), the Azores (Fürsch 1966, 1987; Soares et al. 2003a) and Madeira (Bielawski 1963; Fürsch 1987; Soares et al. 2003b).

Remarks. Two *N. flavopictus* specimens collected at El Monacal have a distinct color form depicted in Fig. 3G. In this form the black markings on the light area of the elytra are missing (for comparison with typically colored individuals see fig. 5K in Romanowski et al. 2019).

***Nephus (Nephus) incisus* (Har. Lindberg, 1950)**

Material examined. La Restinga (8.IV.2019), 11 exx. on *N. oleander* and *Hibiscus* sp.; Montaña del Lajura (8.IV.2019), 2 exx. on *Euphorbia* sp.; Tamaduste (11.IV.2019), 1 ex. on *Euphorbia* sp. (leg. J. Romanowski and C. Zmuda).

Distribution. Endemic Canarian species (Oromí et al. 2010; Romanowski et al. 2019, 2020). By some authors (Fürsch 1987; Eizaguirre 2007; Nicolas 2010) erroneously reported under the name *Nephus peyerimhoffi* (Sicard, 1923) (Romanowski et al. 2019). New to El Hierro.

***Rhyzobius litura* (Fabricius, 1787)**

Material examined. Sabinar (8.IV.2019), 1 ex. on *Juniperus* sp. (leg. J. Romanowski and C. Zmuda).

Distribution. Palaearctic species (Kovář 2007), reported from all the Canary Islands (Eizaguirre 2007; Oromí et al. 2010).

***Rhyzobius lophanthae* (Blaisdell, 1892)**

Material examined. El Mocanal (9.IV.2019), 1 ex.; El Tomillar (7.IV.2019), 1 ex.; Guarazoca (9.IV.2019), 20 exx.; Las Playas (12.IV.2019), 2 exx.; La Restinga (8.IV.2019), 1 ex.; Mirador de Isora (12.IV.2019), 2 exx.; Tigaday (07.IV.2019), 1 ex., collected mostly from *Cycas* sp., *Phoenix canariensis* H. Wildpret, *Hibiscus* sp. and *Yucca* sp. (leg. J. Romanowski and C. Zmuda).

Distribution. Widely distributed species of Australian origin, known from all Canarian Islands (Eizaguirre, 2007).

***Scymnus (Pullus) canariensis* Wollaston, 1864**

Fig. 3F

Material examined. Pozo de la Salud (28.I.2017), 6 exx. (leg. J. Krátký), 2 exx. (leg. J. Pelikán); Sabinosa (28.I.2017), 2 exx. (leg. J. Krátký); Pista del Derrabado (23.I.2017), 1 ex. (leg. J. Krátký); El Chirgo (28.I.2017), 6 exx. (leg. J. Krátký), (29.I.2017), 7 exx. (leg. J. Pelikán); Las Playas (1.II.2017), 2 exx. (leg. J. Krátký); Tamaduste (30.I.2017), 1 ex. (leg. J. Krátký), Camino de Jinama (31.I.2017), 1 ex. (leg. J. Pelikán); Cueva de Don Juste, Echedo, El Juan, El Mocanal, El Sabinal, El Tomillar, Guarazoca, Hoya del Morcillo, Isora, La Caleta, La Dehesa, La Restinga, Las Playas, Mirador de Isora, Montaña de la Casilla, Montaña del Lajura, Pozo de la Salud, Pozo de las Calcosas, Punto de la Dehesa, Sabinar, Tamaduste, Tigaday, Valverde (7–12.IV.2019), total of 901 exx. collected from various plants including *Pinus canariensis* C. Smith, *Juniperus* sp., *N. oleander*, *Prunus dulcis* (Mill.) D.A. Webb, *Casuarina equisetifolia* L., *Hibiscus* sp., *Ph. canariensis*, *Euphorbia* sp., *Hedera* sp. and *Yucca* sp. (leg. J. Romanowski and C. Zmuda).

Distribution. *Scymnus canariensis* has been considered an endemic Canarian species, known from all islands of the archipelago (Eizaguirre 2007). However, recently it was also reported from São Tomé and Príncipe, and Senegal (Hounkpati et al. 2020).

Remarks. On El Hierro, *S. canariensis* has a distinct color form, which is depicted on Fig. 3F. It was already emphasized by Wollaston (1864) that the occurrence of this form (named by him *S. canariensis* var. β) is limited

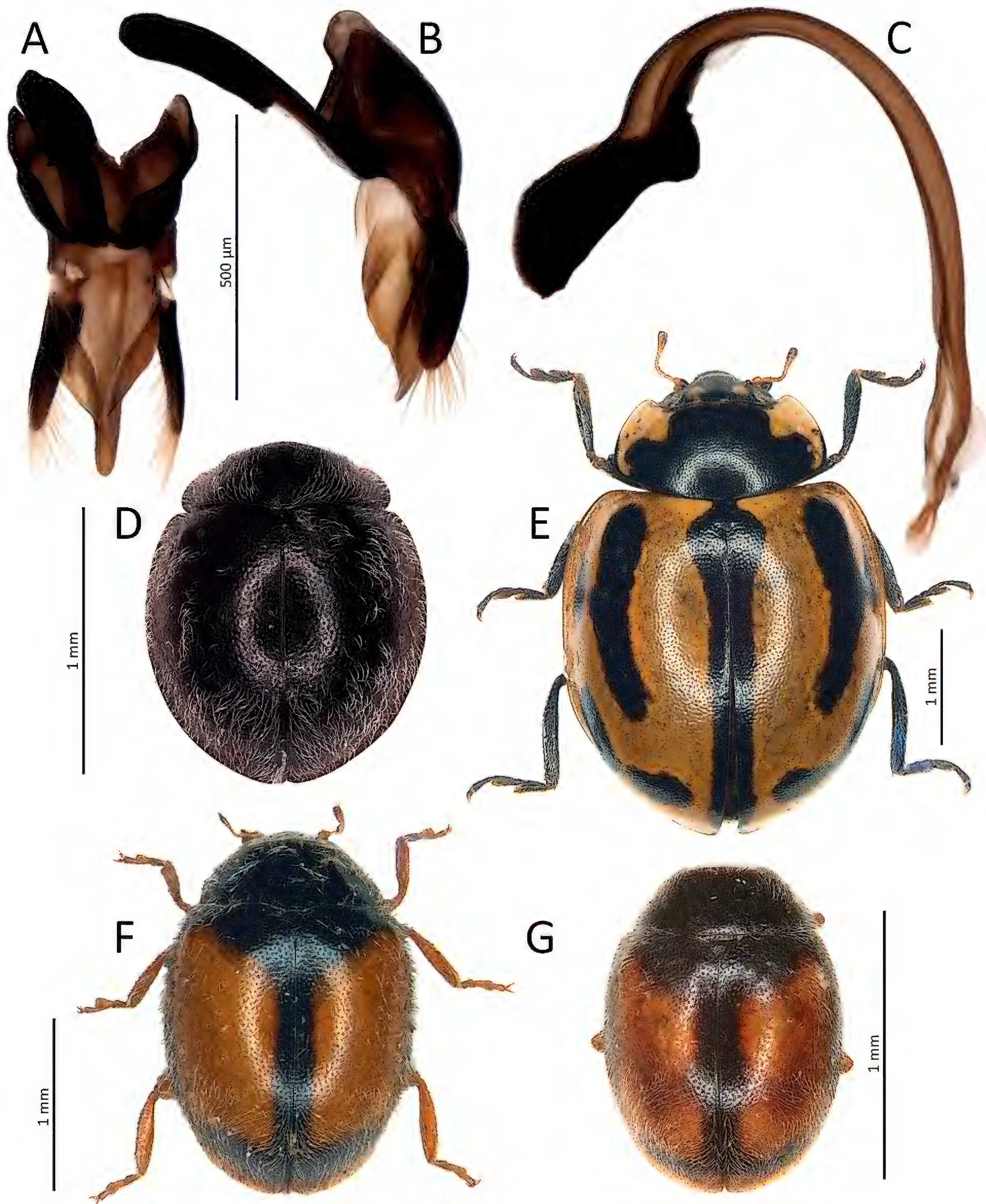


Fig. 3. A–C. *Coccinella miranda* Wollaston. A. Tegmen, inner. B. Tegmen, lateral. C. Penis, lateral. D. *Pharoscymnus decemplagiatus* (Wollaston), habitus of untypically colored specimen from El Hierro. E. *Coccinella miranda* Wollaston, habitus. F. *Scymnus canariensis* Wollaston, habitus of El Hierro color form. G. *Nephus flavopictus* (Wollaston), habitus of untypically colored specimen from El Hierro.

to El Hierro. Male genitalia in this form agree with those of *S. canariensis* from other islands of the archipelago (e.g., Romanowski et al. 2019).

***Scymnus (Mimopullus) cercyonides* Wollaston, 1864
new combination**

Fig. 4A–I

Material examined. El Chirgo (28.I.2017), 5 exx. (leg. J. Krátký) from *Euphorbia* sp., 1 ex. (leg. J. Pelikán); Sabinosa (29.I.2017), 2 exx. (leg. J. Krátký), 1 ex. (leg. J. Pelikán); Eremita de San Salvador (31.I.2017), 1 ex. (leg. J. Krátký) from *Laurus* sp.; El Mocanal (9.IV.2019), 1 ex. from *Hibiscus* sp.; El Tomillar (7.IV.2019), 1 ex. from *Ficus carica* L.; Sabinar (8.IV.2019), 1 ex. from *Juniperus* sp. (leg. J. Romanowski and C. Zmuda).

Distribution. The species reported from western and central Canary Islands (Eizaguirre 2007; Oromí et al. 2010).

Remarks. Male genitalia of our specimens (Fig. 4D–F) are identical with the lectotype drawn by Fürsch (1987). Species frequently misidentified with *Scymnus marinus* Mulsant, 1850. So far it was assigned to the subgenus *Pullus* Mulsant, 1846. However, based on the short carinae on prosternal process, complete and recurved post-coxal abdominal lines (Fig. 4A), and antennae consisting of 11 antennomeres, with a club composed of 4 antennomeres (Fig. 4H), we transfer this species to the subgenus *Mimopullus* Fürsch, 1987.

***Scymnus (Scymnus) nubilus* Mulsant, 1850**

Material examined. Sabinosa (28.I.2017), 1 ex. (leg. J. Krátký); Las Playas (12.IV.2019), 5 exx. on *N. oleander* (leg. J. Romanowski and C. Zmuda).

Distribution. Reported from all the islands of the Canary archipelago except La Palma (Oromí et al. 2010; Romanowski et al. 2019, 2020b). Species widely distributed in the Mediterranean and Middle Eastern regions (Kovář 2007). Recorded also in Pakistan (Gilgit-Baltistan) (Ashfaq et al. 2015), India (Poorani & Lalitha 2018) and Nepal (Bielawski 1972).

***Stethorus tenerifensis* Fürsch, 1987**

Material examined. Eremita de San Salvador (31.I.2017), 1 ex. (leg. J. Pelikán); Echedo, El Mocanal, El Sabinal, El Tomillar, Isora, La Caleta, La Dehesa, La Restinga, Las Playas, Mirador de Isora, Pozo de las Calcosas, Sabinar, Tamaduste, Tigaday, Valverde (7–12.IV.2019), total of 132 exx. collected from various plants

including *Juniperus* sp., *P. canariensis*, *Euphorbia* sp., *N. oleander*, *Ph. canariensis*, *Yucca* sp., *Punica granatum* L. and *F. carica* L. (leg. J. Romanowski and C. Zmuda).

Distribution. Endemic species, known from all Canarian Islands (Eizaguirre 2007; Oromí et al. 2010; Romanowski 2020b).

Coccinellini Latreille, 1807

***Coccinella miranda* Wollaston, 1864**

Fig. 3A–C, E

Material examined. El Greeting (29.I.2017), 1 ex. (leg. J. Krátký); Montaña del Gajo (30.I.2017), 2 exx. (leg. J. Krátký); El Pinar (30.I.2017), 1 ex. (leg. J. Krátký); El Tomillar, Malpaso, Mirador de las Playas, Montaña de la Casilla, Montaña de Masilva, Montaña de Mercadel, Pozo de la Salud, Sabinar (6–11.IV.2019), total of 99 exx. (98 adults, 1 larva) collected from *P. canariensis* (leg. J. Romanowski and C. Zmuda).

Distribution. Endemic Canarian species, reported from Tenerife, La Gomera, La Palma, Gran Canaria and Fuerteventura (Eizaguirre 2007; Oromí et al. 2010). The occurrence on Fuerteventura was not confirmed in a recent study (Romanowski et al. 2019). New to El Hierro.

***Coccinella septempunctata algerica* Kovář, 1977**

Material examined. El Pinar (30.I.2017), 2 exx. (leg. J. Krátký); El Juan, El Mocanal, Hoya del Morcillo, Isora, Las Playas, Mirador de Isora, Mirador de Jinama, Montaña de la Casilla, Pozo de la Salud, San Andres (06–12.IV.2019), total of 67 exx. (66 adults, 1 larva) collected from *P. canariensis*, *Tamarix* sp., *N. oleander* and herbaceous plants (leg. J. Romanowski and C. Zmuda).

Distribution. This Palaearctic species inhabits all seven Canarian islands (Eizaguirre 2007; Oromí et al. 2010).

***Myrrha octodecimguttata* (Linnaeus, 1758)**

Material examined. Árbol Garoé (9.IV.2019), 2 exx. from *P. canariensis*; El Tomillar (7.IV.2019), 1 ex. from *P. canariensis* (leg. J. Romanowski and C. Zmuda).

Distribution. Palaearctic species (Kovář 2007), reported so far from two Canarian islands, La Gomera (Eizaguirre 2007; Oromí et al. 2010) and Gran Canaria (Romanowski et al. 2020a). New to El Hierro.

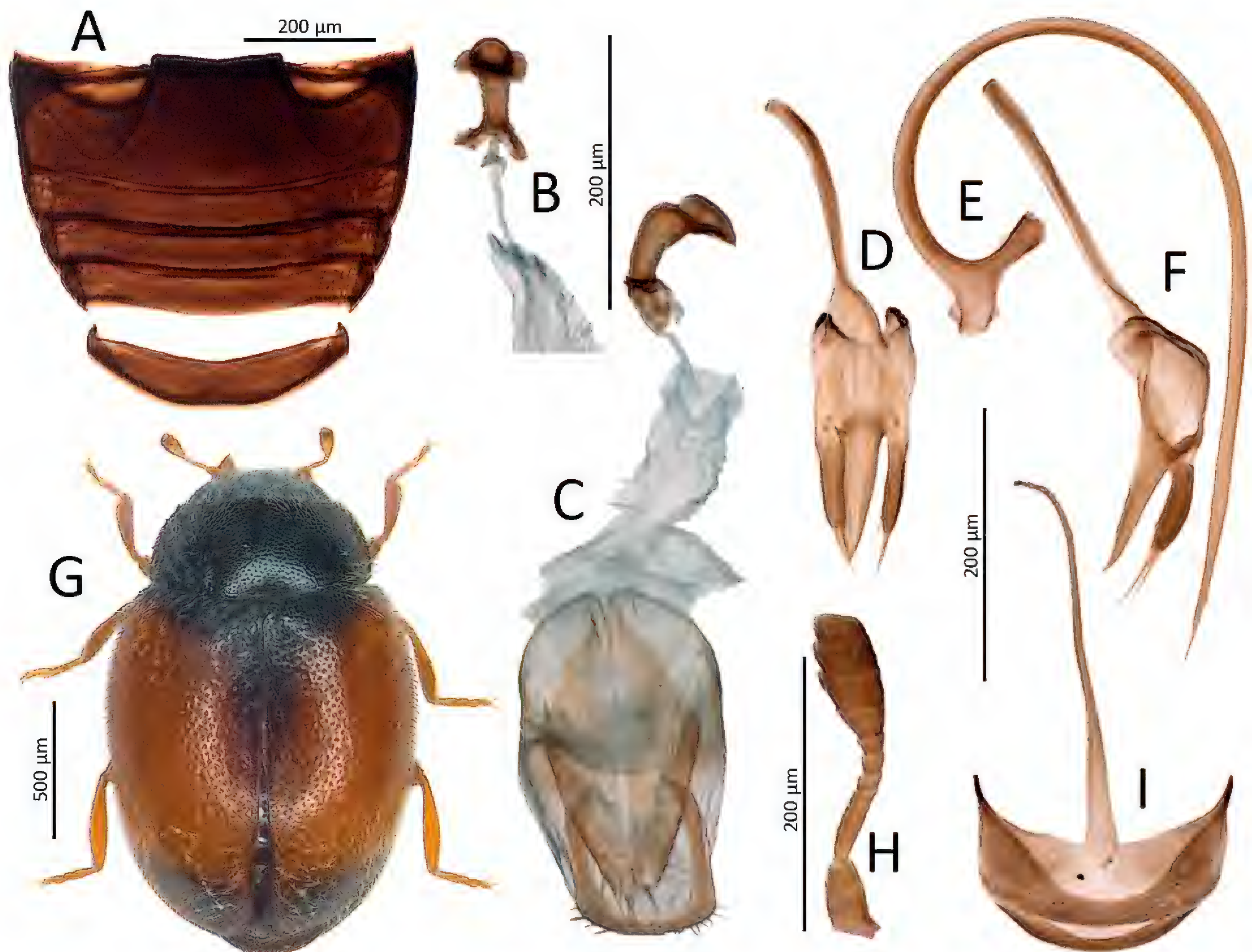


Fig. 4. *Scymnus (Mimopullus) cercyonides* Wollaston. **A.** Abdomen, male. **B.** Spermatheca. **C.** Female genitalia, bursa copulatrix, spermduct and spermathecal. **D.** Tegmen, inner. **E.** Penis, lateral. **F.** Tegmen, lateral. **G.** Habitus. **H.** Antenna. **I.** Male abdominal segments IX and X.

Hippodamia variegata (Goeze, 1777)

Material examined. Isora (12.IV.2019), 1 ex. from *P. granatum*; Montaña de Cascaja (9.IV.2019), 1 ex. from herbaceous vegetation; Pozo de la Salud (7.IV.2019), 4 exx. (3 pupae and 1 larva) from herbaceous vegetation; San Andres (11.IV.2019), 1 ex. from herbaceous vegetation (leg. J. Romanowski and C. Zmuda).

Distribution. The species is widely distributed in the Palearctic, Afrotropical and Oriental regions, and inhabits all seven Canarian islands (Eizaguirre 2007; Oromí et al. 2010).

Noviini Mulsant, 1846

Novius canariensis Korschevsky, 1935

Fig. 5A–F, L

Material examined. Árbol Garoé (9.IV.2019), 1 ex. from *Juniperus* sp.; El Sabinal (7.IV.2019), 1 ex. from *Juniperus* sp.; Mirador de Isora (12.IV.2019), 3 exx. from *Euphorbia* sp.; Tigaday (7.IV.2019), 1 ex. from *Juniperus* sp. (leg. J. Romanowski and C. Zmuda).

Distribution. Endemic Canarian species, known from Tenerife and Gran Canaria (Eizaguirre 2007; Oromí et al. 2010). New to El Hierro.

Remarks. There were some doubts about the validity of this species. Forrester (2008) wrote that she was unable to find and examine the type series of *N. canariensis* collected on Gran Canaria. However, Korschevsky (1935) drew the habitus of that species, which perfectly fits to our specimens collected on El Hierro (Fig. 5L). To check, whether *N. canariensis* is a distinct species, its male genitalia were compared with the genitalia of mainland *N. cruentatus* (Mulsant, 1846) collected in Poland

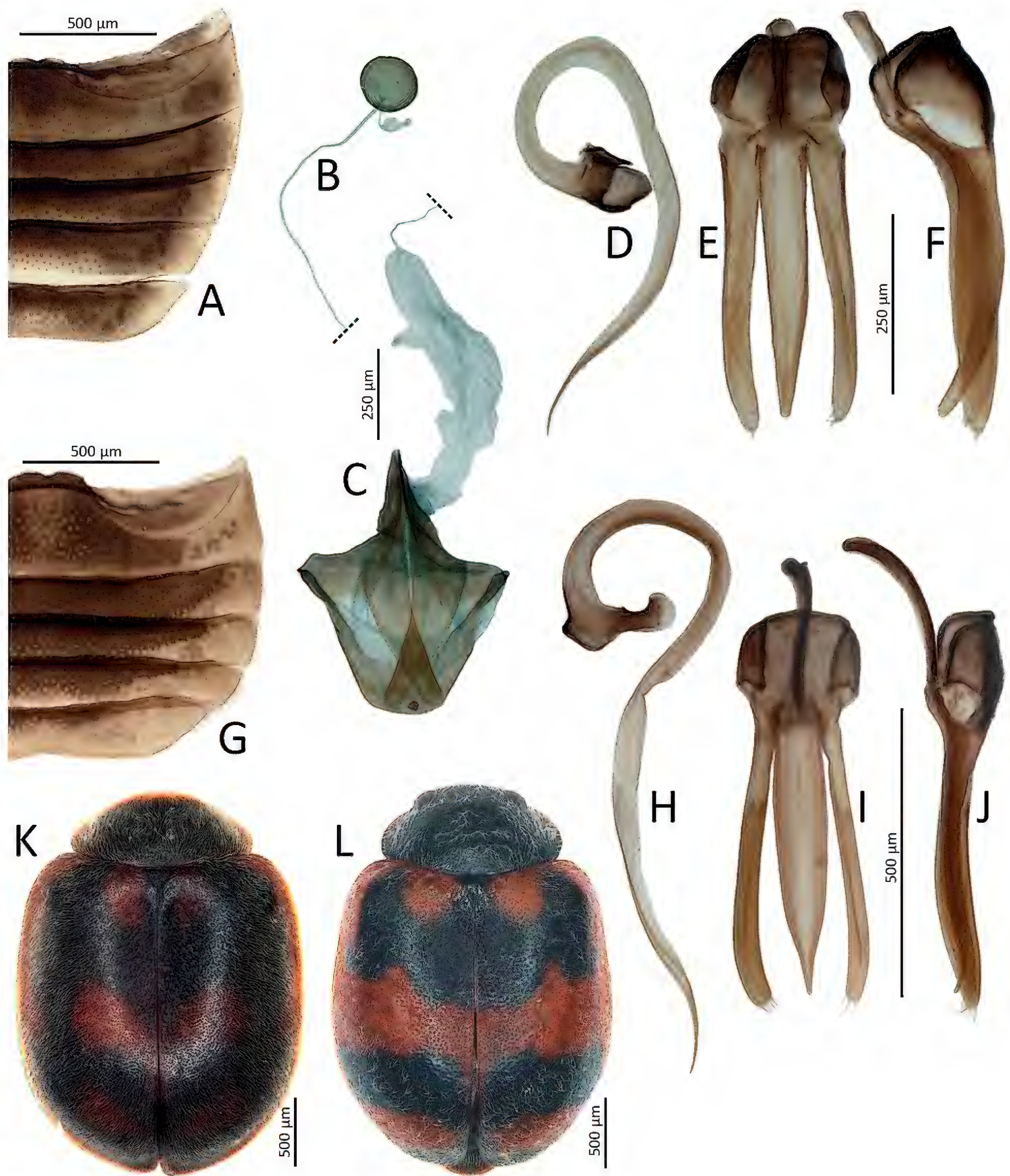


Fig. 5. A–F. *Novius canariensis* Korshefsky. A. Abdomen, male. B. Spermatheca. C. Female genitalia and bursa copulatrix. D. Penis, lateral. E. Tegmen, inner. F. Tegmen, lateral. G–J. *Novius cruentatus* (Mulsant). G. Abdomen, male. H. Penis, lateral. I. Tegmen, inner. J. Tegmen, lateral. K. *Novius cruentatus*, habitus. L. *Novius canariensis*, habitus.

(Fig. 5G–K). Our investigation confirms that the Canarian species is clearly different from *N. cruentatus*.

Differential diagnosis. *Novius canariensis* (Fig. 5L) can be separated externally from *N. cruentatus* (Fig. 5K) by the shape of red maculae on elytra. In *N. canariensis* the central part of elytra is occupied by a complete transverse band, whereas in *N. cruentatus* there are two small red, rounded maculae on each elytron, one close to the lateral margin, second close to sutural line. Sometimes these maculae are larger but they never form complete transverse band. Differences in male genitalia: in *N. canariensis* tegminal strut short, penis guide with blunt apex (Fig. 5E), in lateral view regularly curved (Fig. 5F), in *N. cruentatus* tegminal strut long, penis guide pointed (Fig. 5I), in lateral view sinusoidal (Fig. 5J).

Novius cardinalis (Mulsant, 1850)

Material examined. El Greeting (29.I.2017), 3 exx. (leg. J. Krátký); Camino de Jinama (31.I.2017), 1 ex. (leg. J. Krátký); Valverde (30.I.2017), 1 ex. (leg. J. Krátký); Montaña del Gajo (30.I.2017), 1 ex. (leg. J. Krátký); Cueva de Don Juste (8.IV.2019), 1 ex. from succulents; El Sabinal (7.IV.2019), 1 ex. from *Juniperus* sp.; El Tomillar (7.IV.2019), 6 exx. from *F. carica*; Hoya del Morcillo (6.IV.2019), 1 ex. from *P. canariensis*; La Restinga (8.IV.2019), 2 exx. from *Hibiscus* sp.; Mirador de Isora (12.IV.2019), 4 exx. from *P. dulcis*; Tamaduste (12.IV.2019), 2 exx. from *P. lentiscus*; Tigaday (7.IV.2019), 8 exx. from herbaceous plants (leg. J. Romanowski and C. Zmuda).

Distribution. This species, native to Australia, is currently widely distributed in warmer regions throughout the world (Kovář 2007; Michaud 2012). Reported from all islands of the Canary archipelago (Oromí et al. 2010; Romanowski et al. 2019).

Remarks. This species has for a long time been placed in the genus *Rodolia* Mulsant, 1850. However, *Rodolia* was recently synonymized with *Novius* Mulsant, 1846 (Pang et al. 2020).

Sticholotidini Pope, 1962

Pharoscymnus decemplagiatus (Wollaston, 1857)

Fig. 3D

Material examined. Tamaduste (30.I.2017), 1 ex. (leg. J. Krátký); El Mocanal (9.IV.2019), 4 exx. from *Ficus* sp. and *Hibiscus* sp.; La Caleta (10.IV.2019), 11 exx. from *Euphorbia* sp., *Ficus* sp. and *Hibiscus* sp.; La Restinga (8.IV.2019), 1 ex. from *Hibiscus* sp.; Las Playas (12.IV.2019), 2 exx. from *N. oleander*; Montaña del Lajura (8.IV.2019), 5 exx. from *P. canariensis*; Sabinar

(8.IV.2019), 5 exx. from *Juniperus* sp.; Tamaduste (11.IV.2019), 8 exx. from *Yucca* sp.; Tigaday (8.IV.2019), 9 exx. from *Juniperus* sp. and *Ph. Canariensis* (leg. J. Romanowski and C. Zmuda).

Distribution. Species reported from all islands of the Canary archipelago (Oromí et al. 2010; Romanowski et al. 2019) and from Madeira (Wollaston 1857).

Remarks. One of the specimens of *P. decemplagiatus* collected in this study has a distinct color form depicted in Fig. 3D. It is entirely black, without yellow elytral spots found in typically colored specimens (for comparison see fig. 9B in Romanowski et al. 2019).

DISCUSSION

In this study we recorded the occurrence on El Hierro of 18 species of Coccinellidae, of which four have not previously been reported from the island (Table 2). On the other hand, we failed to find four species reported by other authors: *Scymnus* (*Mimopullus*) *marinus* Mulsant, 1850, *S. (Scymnus)* *rufipennis* Wollaston, 1864, *Stethorus wollastoni* Kapur, 1948 and *Novius cruentatus* (Mulsant, 1846). The total number of ladybird species so far documented to inhabit El Hierro is thus 22. However, the status of the species not recorded in this study (*S. marinus*, *S. rufipennis*, *S. wollastoni* and *N. cruentatus*) needs further investigation. Of the species newly reported for El Hierro, three (*Nephus incisus* *Novius canariensis* and *Coccinella miranda*) are the Canarian endemics, and the fourth (*Myrrha octodecimguttata*) is widely distributed in the Palaearctic region (Kovář 2007).

Although the number of ladybird species known from El Hierro increased slightly as a result of our survey, it is still the lowest among the main seven islands of the archipelago. Not much higher numbers were recorded on Lanzarote (Romanowski et al. 2020b) and La Gomera (Oromí et al. 2010) (23 species on each island), as well as on La Palma (Oromí et al. 2010) (25 species), while clearly higher on Gran Canaria (Romanowski et al. 2020a) (42 species) and Tenerife (Eizaguirre 2007; Oromí et al. 2010; Suarez et al. 2018) (41 species). The low ladybird species richness on El Hierro may be related to the island's small size, low age and long distance from the African continent. On the other hand, relatively few alien species have so far been recorded on El Hierro. Those include three widely distributed Australian species: *Cryptolaemus montrouzieri*, *Rhyzobius lophanthae* and *Novius cardinalis*. In contrast, on Lanzarote, apart from these three Australian species, the American *Delphastus catalinae* (Horn, 1895) and *Olla v-nigrum* (Mulsant, 1866) as well as the Asiatic *Pharoscymnus flexibilis* (Mulsant, 1853) have been found (Romanowski et al. 2020b). The latter two species probably arrived to

Table 2. The list of Coccinellidae recorded on El Hierro in this study and reported in previous papers. Question mark after a reference number means that the presence of a given species on El Hierro was questioned by the author(s) of the quoted paper. Species new to El Hierro in bold print.

No.	Species	This study	Literature data
1	<i>Chilocorus canariensis</i> Crotch, 1874	+	1, 2, 6, 7, 8, 10, 11, 12
2	<i>Parexochomus nigripennis</i> (Erichson, 1843)	+	1, 2, 6, 7, 8, 9 ¹
3	<i>Cryptolaemus montrouzieri</i> Mulsant, 1853	+	1, 7, 8
4	<i>Nephus flavopictus</i> (Wollaston, 1854)	+	2 ² , 3, 4, 6, 8
5	<i>Nephus incisus</i> (Lindberg, 1950)	+	–
6	<i>Rhyzobius litura</i> (Fabricius, 1787)	+	2, 6, 7?, 8, 11, 12
7	<i>Rhyzobius lophanthae</i> (Blaisdell, 1892)	+	2, 6, 7, 8
8	<i>Scymnus (Pullus) canariensis</i> Wollaston, 1864	+	1, 2, 6, 7, 8, 10, 11, 12
9	<i>Scymnus (Mimopullus) cercyonides</i> Wollaston, 1864	+	1, 2, 3, 6, 7, 8, 12
10	<i>Scymnus (Mimopullus) marinus</i> Mulsant, 1850	–	1, 2 ³ , 3, 6, 7, 8
11	<i>Scymnus (Scymnus) rufipennis</i> Wollaston 1864	–	1, 4, 6, 7, 8
12	<i>Scymnus (Scymnus) nubilus</i> Mulsant, 1850	+	1, 2 ⁴ , 6 ⁴ , 7, 8
13	<i>Stethorus tenerifensis</i> Fürsch, 1987	+	1, 3, 6, 7, 8
14	<i>Stethorus wollastoni</i> Kapur, 1948	–	1, 6, 7, 8, 11 ⁵ , 12 ⁵
15	<i>Coccinella miranda</i> Wollaston 1864	+	–
16	<i>Coccinella septempunctata algerica</i> Kovář, 1977	+	2, 5, 6, 7?, 8, 9, 11, 12
17	<i>Myrrha octodecimguttata</i> (Linnaeus, 1758)	+	–
18	<i>Hippodamia variegata</i> (Goeze, 1777)	+	1, 7, 8
19	<i>Novius canariensis</i> Korschefsky, 1935	+	–
20	<i>Novius cruentatus</i> (Mulsant, 1846)	–	1, 2, 6?, 7, 8
21	<i>Rodolia cardinalis</i> (Mulsant, 1850)	+	4, 6, 7?, 8
22	<i>Pharoscymnus decemplagiatus</i> (Wollaston, 1857)	+	1, 4, 6, 7, 8

¹ reported as *Exhochomus* (sic!) *flavipes*

² reported as *Nephus fractus* Wollaston

³ reported as *Pullus pallidivestis* Muls.

⁴ reported as *Scymnus levaillandi* (sic!) Muls. (2) and *S. levaillanti* Mulsant, 1850 (6)

⁵ reported by Wollaston as *Scymnus minimus* (Rossi), a synonymic name of *Stethorus pusillus* (Herbst, 1797). Later Kapur (1948) included the specimens collected by Wollaston in a newly described *S. wollastoni*.

References: 1 – Eizaguirre (2007), 2 – Franz (1995), 3 – Fürsch (1987), 4 – Israelson et al. (1982), 5 – Kovář (1977), 6 – Machado & Oromi (2000), 7 – Nicolas (2010), 8 – Oromi et al. (2010), 9 – Torres del Castillo et al. (1992), 10 – Uyttenboogaart (1935), 11 – Wollaston (1864), 12 – Wollaston (1865)

the Canary Islands very recently: *O. v-nigrum* was first time recorded in the archipelago in 2014 (Tenerife and La Palma) (as *Harmonia axyridis* (Pallas, 1773), see Romanowski et al. 2020a) and *P. flexibilis* in 2016 (Fuerteventura) (Romanowski et al. 2018). It can be assumed that in the near future these newcomers will also reach the western islands of the Canary archipelago, including El Hierro.

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Revision of the aquatic dance flies (Diptera: Empididae: Clinocerinae) described by F. Vaillant in two 1960 publications

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Abstract. The specimens from two 1960 publications by François Vaillant on aquatic empids (Diptera: Empididae: Clinocerinae) are examined. Lectotypes are designated for *Atalanta minutissima* Vaillant, 1960, *A. orientalis* Vaillant, 1965, *A. stackelbergi* Vaillant, 1960, *Oreothalia rupestris* Vaillant, 1960, *Wiedemannia bicolorata* Vaillant, 1960, *W. foliacea* Vaillant, 1960, *W. fumosa* Vaillant, 1960, *W. saltans* Vaillant, 1960, *W. similis* Vaillant, 1960, *Seguyella rostrata* Vaillant, 1960 and *S. tadjikistana* Vaillant, 1960. The following taxonomic changes are proposed: *Atalanta nigra orientalis* Vaillant, 1965 is now *Clinocera orientalis* (Vaillant, 1965), stat. rev. and *Clinocera vaillantiana* sp. nov. is named for *Atalanta* (*Atalanta*) *rufipes sensu* Vaillant.

Key words. Palaearctic, Nearctic, new species, lectotypes, aquatic dance flies.

INTRODUCTION

The French entomologist François Vaillant (1920–) described a series of new species of aquatic empids (Clinocerinae) in two 1960 publications. Vaillant (1960a) listed new distribution records and described three new species from specimens he collected in Tennessee, USA and later Vaillant (1960b) published new species records, a new genus and eight new species from Kazakhstan, Tajikistan and Turkmenistan from specimens borrowed from the Zoological Institute of Russian Academy of Sciences in St. Petersburg. In the latter publication, a portion of the specimens upon which these species were based were retained in his private collection and most of the loaned material was returned. Unfortunately, the material that was returned was inadequately labelled and determination of the type status was hindered by the inability to assemble the entire type series for each species.

Between 2010 and 2013, the private Diptera, Coleoptera and Trichoptera collections of François Vaillant, representing around 12,000 slides and numerous pinned specimens, were donated to the Musée cantonal de zoologie, Lausanne, Switzerland (MZLS). Among this valuable collection were around 1,300 slides of Empididae including type material for about 70 species. This study

of the Clinocerinae specimens from the 1960 publications was initiated to answer several long outstanding questions for BJS and IVS and represents only a small portion of the aquatic dance fly collection. This is a follow-up study to Sinclair & Shamshev (2019) which investigated only a short series of specimens determined as *Wiedemannia lota* Walker, 1851. Much work remains in identifying all the type specimens from this vast donation.

MATERIAL AND METHODS

This study is based on material housed in the Musée cantonal de zoologie, Lausanne, Switzerland (MZLS) and the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia (ZIN).

The label data for type specimens are cited verbatim and listed beginning with the top label continuing to the bottom label. Data on labels are listed within quotation marks, with a change in label represented by a semicolon. A new line on a label is indicated by a slash (/). Any additional information not found on the labels is given in square brackets.

The status of the type material of the new species described in Vaillant (1960a, b) was not distinctly outlined.

For several species there was no statement concerning name-bearing types and in these cases all specimens listed are treated as syntypes according to the International Code of Zoological Nomenclature (ICZN 1999) Article 73.2.1. In most cases, Vaillant (1960a, b) used the expression “type choisi du ...” to indicate either the type locality or the collection locality of a type specimen, and in our opinion this was not an explicit statement of type fixation. The identification of the name-bearing specimen was further inhibited by the lack of explicit labelling. Although all specimens examined by us bear Vaillant’s determination label, no “type” labels were attached. The ICZN (1999) Article 73.1.1 states: “If an author when establishing a new nominal species-group taxon states in the original publication that one specimen, and only one, is the holotype, or “the type” [French version of ICZN: “le type”], or uses some equivalent expression, that specimen is the holotype fixed by original designation”. On the basis of the use of the above expression by Vaillant without a definite article, in combination with the absence of type labelling, we interpret that a particular name-bearing specimen was not established in these publications. All specimens listed by Vaillant under material examined sections are treated as syntypes. A similar interpretation of type material status was discussed by Richet et al. (2013).

RESULTS

Material from Vaillant (1960a)

During a visit to Tennessee (USA) in August 1955, Vaillant collected aquatic insects from streams and waterfalls in Great Smoky Mountains National Park of Tennessee and North Carolina (USA). This material later formed the basis of several publications on Thaumaleidae (Vaillant 1959a), Psychodidae (Vaillant 1959b) and Clinocerinae (Empididae) (Vaillant 1960a). In the latter publication, Vaillant (1960a) described three new species. The following species were listed in this publication and all specimens associated with his identifications were studied if available. All material was poorly labelled in terms of type material and the depository of the types was not specified in the publication. Fortunately, Vaillant’s descriptions and illustrations have readily facilitated species identification by subsequent taxonomists without the need for direct comparisons with type specimens.

Clinocera sp.

Atalanta (Hydrodromia) sp.: Vaillant, 1960a: 119.

Material. Le Comte, 10.viii.1955 (1 ♀).

Remarks. The genus name *Atalanta* Meigen, 1800 was suppressed by the ICZN (1963) and Sinclair (1995) listed the subgenus *Hydrodromia* Macquart, 1835 as a junior synonym of *Clinocera* Meigen, 1803.

The single female specimen listed by Vaillant (1960a) was not found among the donated collection.

Roederiodes recurvatus Chillcott, 1961

(Fig. 1)

Roederiodes recurvatus Chillcott, 1961: 424. Type locality: Old Chelsea, Quebec, Canada.

R. recurvatus: Melander, 1965: 468 (catalogue); Wilder, 1981a: 419 (review); Sinclair, 1995: 698 (checklist).

Roederiodes junctus Coquillett, 1901: Vaillant, 1960a: 117 (not Coquillett) (Wilder 1981a: 419).

Material examined. USA. Tennessee: Roaring Fork Creek [near Gatlinburg, 600 m], 20.viii.1955, F. Vaillant (slides: GBIFCH00606816: 1 ♂, 2 ♀♀; GBIFCH00606817: 1 ♂; GBIFCH00606818: 2 ♂♂; pinned: GBIFCH00654925: 1 ?♂ [abdomen missing]; all MZLS).

Remarks. Vaillant (1960a) identified and labelled the above material as *Roederiodes junctus* (Fig. 1). This was a misidentification of *R. recurvatus* (see Chillcott 1961: fig. 17).

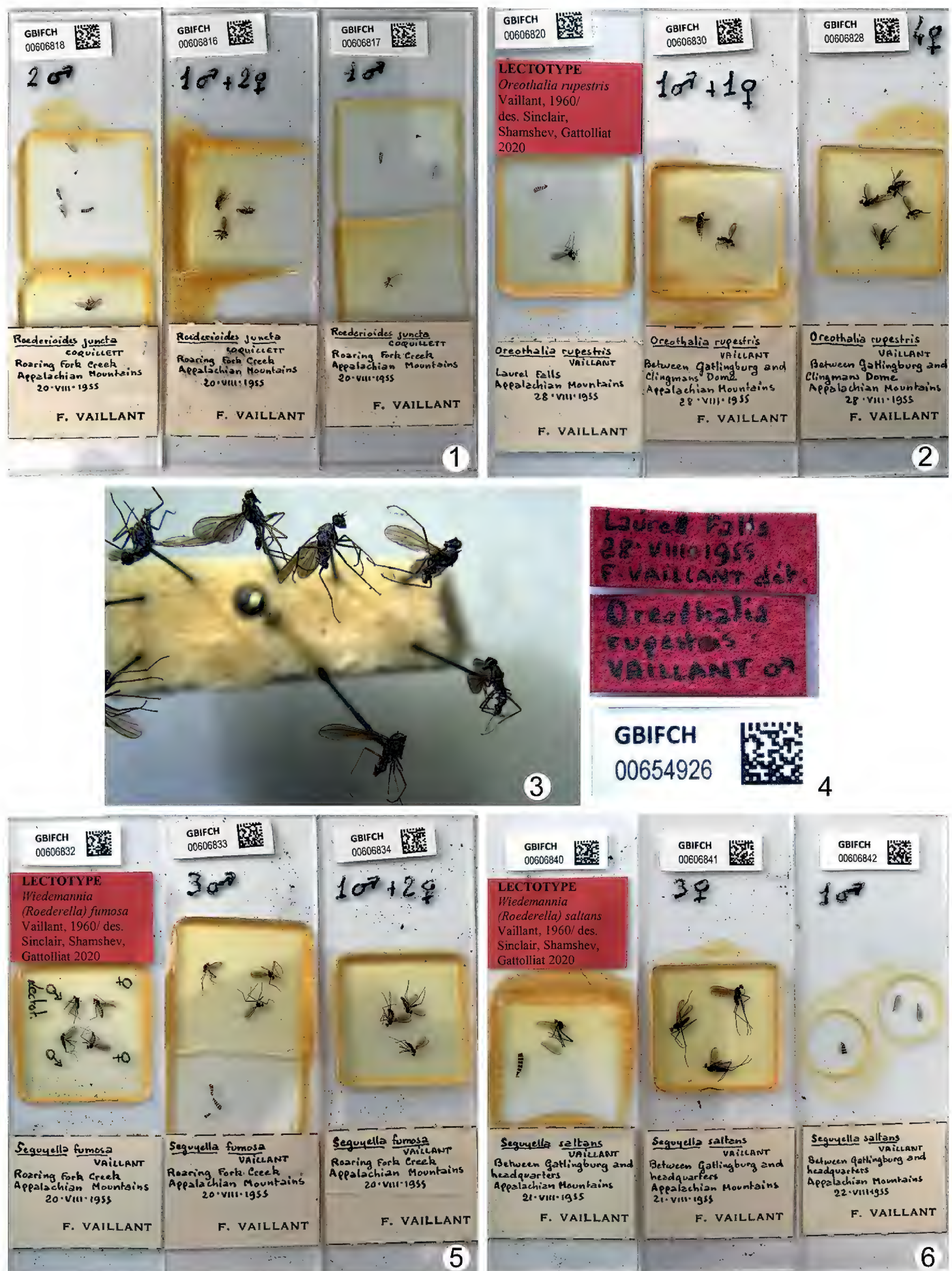
Oreothalia rupestris Vaillant, 1960

(Fig. 2)

Oreothalia rupestris Vaillant, 1960a: 118. Type locality (by lectotype designation): Laurel Falls, Tennessee, USA.

O. rupestris: Melander, 1965: 467 (catalogue); Wilder, 1981b: 463 (revision); Sinclair, 1995: 696 (checklist).

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled (Fig. 2): “GBIFCH/ 00606820”; “LECTOTYPE/ *Oreothalia rupestris*/ Vaillant, 1960// des. Sinclair,/ Shamshiev, Gattolliat/ 2020 [red label]”; “*Oreothalia rupestris*/ VAILLANT/ Laurel Falls/ Appalachian Mountains/ 28.VIII.1955, F. VAILLANT” (MZLS, slide). **PARALECTOTYPES: USA. Tennessee:** same data as lectotype except, GBIFCH00606821 (1 ♂, MZLS, slide); same data except, GBIFCH00606822 (1 ♂, MZLS, slide); same data except, GBIFCH00606823 (1 ♂, 1 ♀, MZLS, slide); same data except, GBIFCH00606824 (1 ♂, 1 ♀, MZLS, slide); same data except, GBIFCH00606825



Figs 1–6. Specimens from Vaillant (1960a). 1. *Roederioides junctus* (= *R. recurvatus* Chillcott), three slides. 2. *Oreothalia rupestris* Vaillant, lectotype and two paralectotype slides. 3. *O. rupestris* Vaillant, pinned males. 4. *O. rupestris* Vaillant, labels on pin. 5. *Wiedemannia fumosa* Vaillant (= *Trichoclinocera fumosa*), lectotype and two paralectotype slides. 6. *Wiedemannia saltans* Vaillant (= *Trichoclinocera hamifera* (Melander)), lectotype and two paralectotype slides.

(1 ♂, 1 ♀, MZLS, slide); same data except, GBIFCH00606826 (1 ♂, MZLS, slide); same data except, GBIFCH00606827 (1 ♂, 1 ♀, MZLS, slide); Gatlinburg to Clingmans Dome Rd., 900 m, 28.viii.1955, F. Vaillant (slides: GBIFCH00606828: 4 ♀♀, GBIFCH00606829: 1 ♂, GBIFCH00606830: 1 ♂, 1 ♀; all MZLS); Mt. Le Conte, 10.viii.1955, 1950 m, F. Vaillant (slide: GBIFCH00606831: 1 ♂, MZLS).

Additional material. USA. Tennessee: Laurel Falls, 28.viii.1955, F. Vaillant (pinned: GBIFCH00654926: 8 ♂♂, GBIFCH00654927: 9 ♀♀, MZLS; 3 empty pins without specimens, ZIN).

Remarks. Vaillant (1960a) designated Laurel Falls as the type locality (8 males and 4 females) and all specimens were found mounted on slides, but the collection date was published as 20 August instead of 28 August as stated on the labels (Fig. 2). The pinned specimens from Laurel Falls (Figs 3, 4) listed under Additional material were not reported among the material examined by Vaillant (1960a) and are not considered part of the original syntype series. Vaillant donated some specimens to ZIN but we found only empty pins.

Oreothalia rupestris is the only described species of this endemic Nearctic genus in the East, occurring only in the Great Smoky Mountains (Wilder 1981b; Sinclair unpubl. data). There is a probable undescribed species based on a single female specimen from Gainesville, Florida, distinguished from *O. rupestris* on the basis of wing venation, pleural colouration and chaetotaxy (Sinclair 1995).

***Trichoclinocera fumosa* (Vaillant, 1960)**
(Fig. 5)

Wiedemannia (*Roederella*) *fumosa* Vaillant, 1960a: 119.

Type locality (by lectotype designation): Roaring Fork Creek, Great Smoky Mountains, Tennessee, USA.

W. (Roederella) fumosa: Melander, 1965: 469 (catalogue).

Seguyella fumosa (Vaillant): Vaillant, 1960b: 180 (new combination).

Trichoclinocera fumosa (Vaillant): Sinclair, 1994: 1029 (new combination, revision).

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled (Fig. 5): “GBIFCH/ 00606832”; “LECTOTYPE/ *Wiedemannia* (*Roederella*) *fumosa*/ Vaillant, 1960/ des./ Sinclair, Shamshev,/ Gattolliat 2020 [red label]”; “*Seguyella fumosa*/ VAILLANT/ Roaring Fork Creek/ Appalachian Mountains [Great Smoky Mountains National Park]/ 20.VIII.1955/ F. VAILLANT” (MZLS, upper left specimen). **PARALECTOTYPES: USA. Tennessee:** on same slide as lectotype (1 ♂, 2 ♀♀, MZLS, slide);

same data except, GBIFCH00606833 (3 ♂♂, MZLS, slide); same data except, GBIFCH00606834 (1 ♂, 2 ♀♀, MZLS, slide); same data except, GBIFCH00606835 (1 ♂, 2 ♀♀, MZLS, slide); same data except, GBIFCH00606836 (2 ♂♂, 3 ♀♀, MZLS, slide); Little River, 3000 ft [1100 m, F. Vaillant], GBIFCH00654928 (1 ♂, 1 ♀, MZLS, pinned together on single mount).

Remarks. Vaillant (1960a) designated Roaring Fork Creek as the type locality (16 males and 24 females) and 10 males and 8 females were located for this study.

Vaillant (1960b) transferred *Wiedemannia fumosa* to a new genus, *Seguyella* Vaillant, 1960b, which is now classified as a junior synonym of *Trichoclinocera* Collin, 1941 (Sinclair 1994). This species was transferred to *Trichoclinocera* and redescribed by Sinclair (1994), where the species was shown to occur primarily in the southern Appalachian Mountains from Virginia to northern Georgia.

***Trichoclinocera hamifera* (Melander, 1928)**
(Fig. 6)

Wiedemannia (*Chamaedipsia*) *hamifera* Melander, 1928: 233. Type locality: Beaverkill, New York, USA.

Wiedemannia (*Roederella*) *saltans* Vaillant, 1960a: 122. Type locality (by lectotype designation): near Gatlinburg, Tennessee, USA.

Wiedemannia (*Chamaedipsia*) *saltans*: Melander, 1965: 469 (catalogue).

Seguyella saltans (Vaillant): Vaillant, 1960b: 180 (new combination).

Trichoclinocera hamifera (Melander): Sinclair, 1994: 1030 (new synonym, revision).

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled (Fig. 6): “GBIFCH/ 00606840” 1 ♂”; “LECTOTYPE/ *Wiedemannia* (*Roederella*) *saltans*/ Vaillant, 1960/ des./ Sinclair, Shamshev,/ Gattolliat 2020 [red label]”; “*Seguyella saltans*/ VAILLANT/ Between Gatlinburg and headquarters [Great Smoky Mountains National Park]/ Appalachian Mountains/ 21.VIII.1955/ F. VAILLANT” (MZLS, slide). **PARALECTOTYPES: USA. Tennessee:** same data as lectotype except, GBIFCH00606841 (3 ♀♀, MZLS, slide); same data except, 22.viii.1955, GBIFCH00606842 (1 ♂, MZLS, slide); Greenbrier Cove [600 m], 17.viii.1955, F. Vaillant (slides: GBIFCH00606837: 3 ♀♀; GBIFCH00606838: 1 ♂; GBIFCH00606839: 2 ♀♀, all MZLS).

Remarks. Vaillant (1960a) designated “between Gatlinburg, Tennessee and the headquarters of the Great Smoky Mountains National Park” (3 males, 3 females) as the type locality and 2 males and 3 females were located for this study.

Vaillant (1960b) transferred *Wiedemannia saltans* to the new genus *Seguyella*. This genus is a junior synonym of *Trichoclinocera* Collin and *S. saltans* is a junior synonym of *Trichoclinocera hamifera* (Sinclair 1994).

Trichoclinocera sp.

Wiedemannia (Philolutra) sp.: Vaillant, 1960a: 123.

Material. Between Gatlinburg and National Park headquarters, 22.viii.1955 (7 ♀♀).

Remarks. The seven female specimens identified by Vaillant were not found among the donated collection. The genus *Wiedemannia* Zetterstedt, 1838 does not occur in the southern Appalachians and we assume that these specimens belong to *Trichoclinocera*. There are at least four species of *Trichoclinocera* present in the southern Appalachian Mountains including *T. falcata* Sinclair, 1994 and *T. minor* (Melander, 1928), in addition to the two species above (Sinclair 1994).

Material from Vaillant (1960b)

Vaillant (1960b) borrowed a series of Clinocerinae specimens collected in central Asia from A.A. Stackelberg (ZIN). Vaillant (1960b) described eight new species, identified four additional species of Clinocerinae and described a new genus, *Seguyella*. Vaillant returned a portion of the original loan and retained an unknown number of specimens from his study for his private collection. All material was poorly labelled in terms of type material and the depository of the types was not specified. Fortunately, Vaillant's descriptions and illustrations have readily facilitated species identification by subsequent taxonomists without the need for direct comparisons with type specimens.

Clinocera minutissima (Vaillant, 1960)

(Fig. 15)

Atalanta (Atalanta) minutissima Vaillant, 1960b: 172.

Type locality (by lectotype designation): Khorog on Gunt River (37°29'N 71°33'E), Tajikistan.

Clinocera minutissima (Vaillant): Chvála & Wagner, 1989: 330 (catalogue); Sinclair, 1995: 693 (checklist).

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled (Fig. 15): [printed in Cyrillic] [Tajikistan]: “Khorog on r. [=reka, river] Gunt/ Shugnan, 25.ix.[1]943./ Stackelberg”; “LECTOTYPE/ *Atalanta (Atalanta) minutissima*/ Vaillant, 1960/ des. Sinclair, Shamshev, Gattolliat 2020 [red label]”; “GBIFCH/ 00596473”; “*Atalanta (Atalanta) minutissima* VAILLANT ♂/ Khorog, Pamir/ occidental. Tadzikistan/ 25.IX.1943/ A.A. STACKELBERG

coll./ F. VAILLANT [hand-written by Vaillant]” (1 ♂, MZLS). **PARALECTOTYPES:** same data as lectotype (2 ♂♂, MZLS, slides; 1 ♀, ZIN, pinned).

Remarks. Vaillant (1960b) designated the locality “Khorog” as the type locality, which included two males and two females. We identified three males and one female from the type series. Vaillant (1960b) also listed a single female from “Kondara”, but this specimen was not found in either MZLS or ZIN.

Sinclair (1995) assigned this species to the *C. lineata* group on the basis of the form of the surstylus (Sinclair 2008). Many species in this group, including *C. minutissima*, possess facial setulae (defining feature of genus *Kowarzia* Mik, 1882), but the male terminalia clearly identify them as belonging to the genus *Clinocera*.

Clinocera orientalis (Vaillant, 1965) stat. rev.

(Figs 7–10)

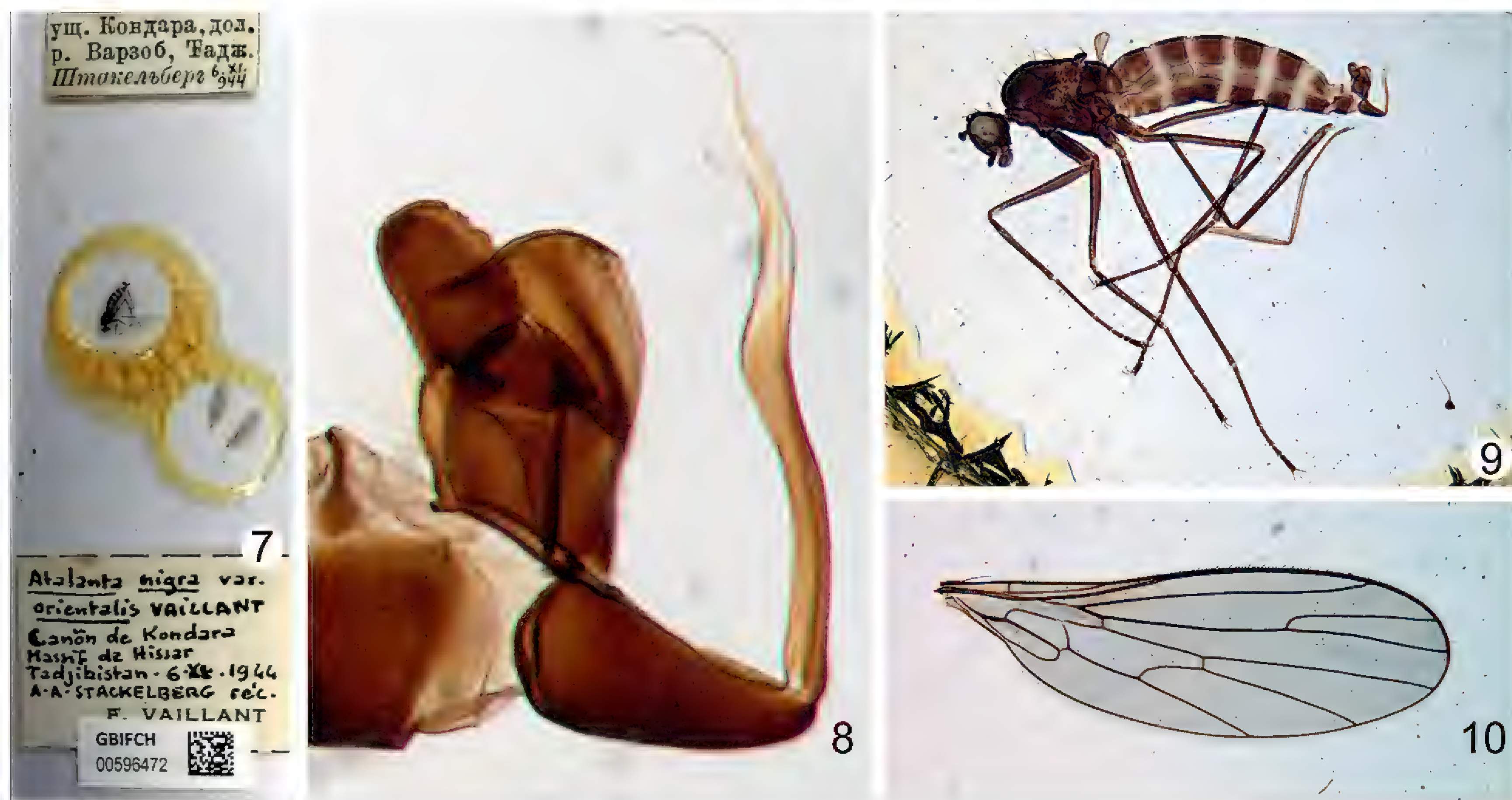
Clinocera nigra Meigen, 1804: Vaillant, 1960b: 174 (as *Atalanta (Atalanta)*).

Atalanta nigra orientalis Vaillant, 1965: 148. Type locality (by lectotype designation): Kondara Canyon, valley of Varzob River (38°48'N 68°48'E), Tajikistan.

Clinocera nigra orientalis (Vaillant): Sinclair, 1995: 693 (checklist).

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled: “[printed in Cyrillic] [Tajikistan] *Atalanta (Atalanta) nigra* (Meigen)/ ♂ [hand-written by Vaillant, yellow label]”; “usch. [=uschelje, canyon] Kondara, dol. [=dolina, valley]/ r. [=reka, river] Varzob, Taj. [=Tajikistan]/ Stackelberg 6.xi.[1]944”; “Lectotypus/ *Atalanta nigra orientalis* Vaillant, 1965/ design. Sinclair, Shamshev, Gattolliat 2020” (ZIN, INS_DIP_0000606). **PARALECTOTYPE:** same data as lectotype, GBIFCH00596472 (1 ♂, slide, MZLS).

Remarks. Vaillant (1960b) initially identified nine specimens from Tajikistan as *C. nigra* Meigen. Vaillant (1965) later re-evaluated his decision and concluded that these Central Asian specimens differed in the male genitalia and named a new subspecies (as *A. (A.) nigra orientalis*) for these specimens. No type or type locality was designated for this new subspecies. We consider the male genitalia of *C. nigra orientalis* (see Vaillant 1965: figs 11, 1m) are sufficiently different from *C. nigra* to warrant elevation to species. Only two of nine specimens listed in Vaillant (1960b) could be found of this species.



Figs 7–10. *Clinocera orientalis* (Vaillant) stat. rev., male paralectotype. 7. Slide. 8. Terminalia. 9. Habitus. 10. wing.

***Clinocera stackelbergi* (Vaillant, 1960)**

(Fig. 16)

Atalanta (*Kowarzia*) *stackelbergi* Vaillant, 1960b: 174.

Type locality (by lectotype designation): Khorog on river Gunt (37°29'N 71°33'E), Tajikistan.

Clinocera (*Kowarzia*) *stackelbergi* (Vaillant): Chvála & Wagner, 1989: 334 (catalogue).

Clinocera stackelbergi (Vaillant): Sinclair, 1995: 693 (checklist).

Type material examined. **LECTOTYPE** (here designated in order to fix identity of the species), ♂ labelled (Fig. 16): “*Atalanta*/ (*Kowarzia*)/ *stackelbergi*/ VAILLANT/ ♂/ F. VAILLANT det. [yellow label, hand-written by Vaillant]”; “[printed in Cyrillic] Khorog na r. [na reke, =on river] Gunt/ Shugnan 25.ix.[1]943, Stackelberg”; “LECTOTYPUS/ *Atalanta* (*Kowarzia*)/ *stackelbergi* Vaillant, 1960/ des. Sinclair, Shamshev, Gattolliat/ 2020 [red label]” (ZIN, INS_DIP_0000607). **PARALECTOTYPES: Tajikistan:** same data as lectotype (2 ♂♂, 1 ♀, ZIN; GBIFCH00602303:1 ♂, MZLS, slide); same data as lectotype except, 26.ix.1943 (1 ♂, ZIN); Kondara Canyon, valley of river Varzob, Stackelberg, 6.xi.1944, GBIFCH00602304 (1 ♂, MZLS, slide).

Remarks. Vaillant (1960b) did not designate a type specimen or type locality for this species. A total of six male and two female syntypes were listed, and six male and one female syntypes were found during this study.

Despite the presence of facial setulae, a defining character of the genus *Kowarzia*, Sinclair (1995) transferred this species to *Clinocera* and assigned it to the *C. lineata* group on the basis of male terminalia.

***Clinocera stagnalis* (Haliday, 1833)**

Heleodromia stagnalis Haliday, 1833: 159. Type locality: Holywood, Downshire, Ireland.

Material examined. Tajikistan: Stalinabad [=Dushanbe] valley of Gulbisty River, 20.iv.1943 (1 ♂, ZIN); Stalinabad [=Dushanbe], loess hills, 24.iv.1943, Stackelberg (1 ♀, ZIN), 5.iv.1944 (1 ♀, ZIN); Stalinabad [=Dushanbe], foothills, 18.iv.1943, Goussakovsky (1 ♀, ZIN); Tavidara, N slope of Darvazskiy Ridge, 10.x.1942 (1 ♂, ZIN); Viskharvi on Pyandzh River, 21.x.1942, Stackelberg (1 ♂, ZIN).

Remarks. This is a very widespread species, found across the Palaearctic Region and the arctic and Rocky Mountains of the Nearctic Region (Sinclair 2008).

***Clinocera vaillantiana* sp. nov.**

(Figs 11–14)

Atalanta (*Atalanta*) *rufipes* Vaillant, 1960b: 174 (not Bezzi).

Type material examined. **HOLOTYPE** ♂, labelled (Fig. 11): “[printed in Cyrillic] [Tajikistan] ush. [=us-



Figs 11–14. *Clinocera vaillantiana* sp. nov., male holotype. 11. Slide. 12. Terminalia. 13. Habitus. 14. wing.

chelje, canyon] Kondara, dol. [=dolina, valley]/ r. [=reka, river] Varzob, Taj. [=Tajikistan]/ Stackelberg 20.iv. [19]44"; "HOLOTYPE/ *Clinocera vaillantiana*/ Sinclair, Shamshev,/ Gattolliat, 2020"; "Atalanta (Atalanta)/ rufipes Bezzi ♂/ Cañon de Kondara/ Massif de Hissar/ Tadzikistan, 20.IV.1944/ A.A. STACKELBERG coll./ F. VAILLANT"; "GBIFCH/ 00596471" (MZLS, slide).

Description. Male. Head with broad face; ocellar seta 3/4 length of scutal setae; postpedicel short ovate; arista-like stylus slender. Scutum with long setae; subequal in length with scutellar setae; 1 postpronotal seta weaker than notopleural setae; 1 presutural postalar seta; 2 notopleural setae; 1 postsutural postalar seta; 6 dorsocentral setae. Legs with coxae and femora pale brown (Fig. 13); remaining legs dark brown; fore femur with biserial row of ventral setae, setae half as long as width of femur; fore tibia with erect ventral setae. Wing infusate (Fig. 14), lacking spots or clouding; pterostigma absent; auxiliary crossveins absent; cell dm produced distally; halter pale brown.

Male terminalia (Fig. 12; Vaillant 1960b: figs 2c–f): Claspings cercus oval, strongly tapered apically. Surstylus digitiform with sharply pointed subapical process. Phallus slightly sinuous, not expanded apically; distiphallus slender and arched.

Etymology. This species is a patronym in honour of François Vaillant in recognition of his efforts to describe the diversity of aquatic empidids and he will be 100 years of age in 2020.

Remarks. Vaillant (1960b: figs 2c–f) considered the single specimen he identified as *Atalanta (Atalanta) rufipes* (Bezzi, 1899) to be significantly different from *C. nigra rufipes* [originally *Atalanta (Atalanta) nigra rufipes*] and consequently elevated *rufipes sensu* Vaillant to species level. Sinclair (2007) examined syntype specimens of *C. rufipes* Bezzi and proposed this species as a junior synonym of *C. nigra*. On the basis of the illustration of the male genitalia of *C. rufipes* in Sinclair (2007: fig. 1), the male genitalia of this Central Asian specimen (Vaillant 1960b: figs 2c–f; Fig. 12) is clearly not conspecific, and represents a new species described herein.

***Trichoclinocera cyanescens* (Vaillant, 1960)**
(Fig. 17)

Seguyella cyanescens Vaillant, 1960b: 180. Type locality: "Tavilj Dara" [= Tavildara] (38°41'N 70°29'E), Tajikistan.

Seguyella cyanescens: Chvála & Wagner, 1989: 322 (catalogue).

Trichoclinocera cyanescens (Vaillant): Sinclair, 1994: 1015 (new combination).

Type material examined. HOLOTYPE ♂, labelled (Fig. 17) [printed in Cyrillic] [Tajikistan]: "Tavil-dara [=Tavildara, 38°41'N 70°29'E], N/ skl. [=sklon, slope] Darvaz. [=Darvazskiy] khr. [=khrebet, ridge] 9,x/ Stackelberg [1]942"; "GBIFCH/ 00606848"; "HOLOTYPE/ Seguyella cyanescens/ Vaillant, 1960"; "Seguyella cyanescens/ VAILLANT ♂/ Tavilj Dara, Massif de/ Darvaz.

Tadzikistan/ 9.X.1942/ A.A. STACKELBERG coll./ F. VAILLANT" (MZLS, slide).

Remarks. This species was described on the basis of a single male specimen. Vaillant removed this specimen from the pin and made a slide mount, including the original locality label. A holotype label has been attached.

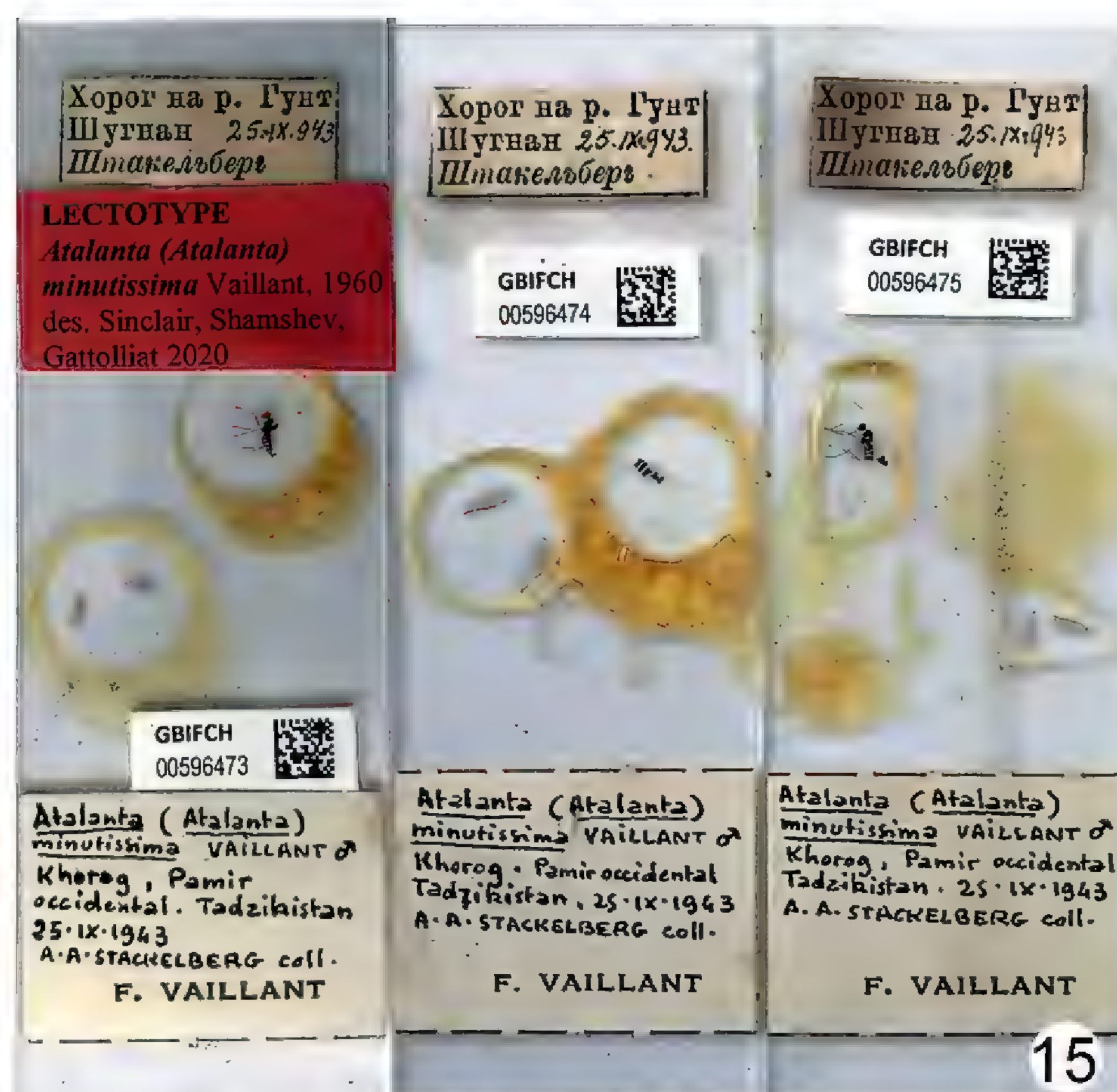
Trichoclinocera rostrata (Vaillant, 1960)

(Fig. 18)

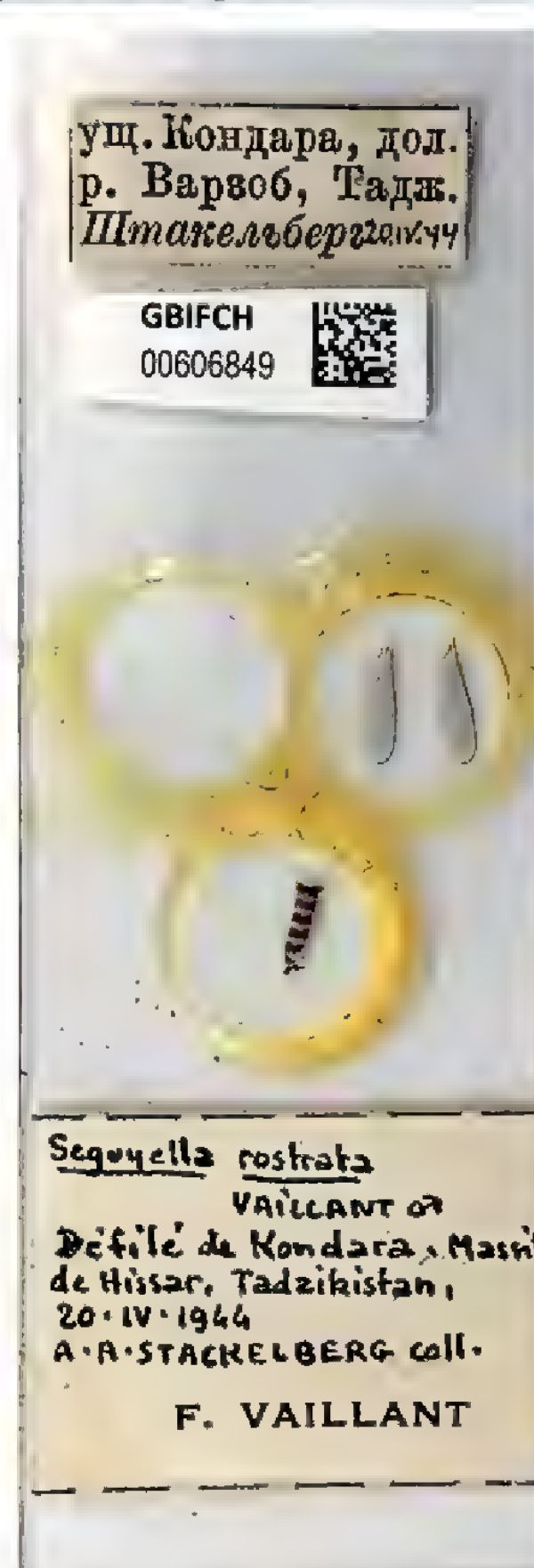
Seguyella rostrata Vaillant, 1960b: 181. Type locality (by lectotype designation): Kondara Canyon, valley of river Varzob (38°48'N 68°48'E), Tajikistan.

Seguyella rostrata: Chvála & Wagner, 1989: 322 (catalogue).

Trichoclinocera rostrata (Vaillant): Sinclair, 1994: 1016 (new combination).



16



18



19

Figs 15–19. Specimens from Vaillant (1960b). 15. *Clinocera minutissima* (Vaillant), lectotype and two paralectotype slides. 16. *Clinocera stackelbergi* (Vaillant), lectotype and labels. 17. *Seguyella cyanescens* Vaillant (= *Trichoclinocera cyanescens*), holotype slide. 18. *Seguyella rostrata* Vaillant (= *Trichoclinocera rostrata*), two paralectotype slides. 19. *Seguyella tadjikistana* Vaillant (= *Trichoclinocera tadjikistana*), paralectotype slide.

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled [printed in Cyrillic] [Tajikistan]: “Seguyella/ rostrata/ VAILLANT/ ♂/ F. VAILLANT det. [yellow label, hand-written by Vaillant]”; “usch. [=uschelje, canyon] Kondara, dol. [=dolina, valley]/ r. [reka, river] Varzob, Tadj. [=Tajikistan]/ Stackelberg 20.iv.[19]44”; “Trichoclinocera/ rostrata/ det. B.J. Sinclair 1993”; “LECTOTYPUS/ Seguyella/ rostrata Vaillant/ des. Sinclair, Shamshev, Gattolliat 2020 [red label]” (ZIN, INS_DIP_0000608). **PARALECTOTYPES: Tajikistan:** same data as lectotype (2 ♂♂, 7 ♀♀, ZIN); same data as lectotype (Fig. 18) (slides: GBIFCH00606849: 1 ♂; GBIFCH00606850: 1 ♂; pinned: GBIFCH00654933: 1 ♀; GBIFCH00654934: 1 ♀; GBIFCH00654935: 1 ♂; all MZLS).

Remarks. Vaillant (1960b) did not designate a type specimen for this species and examined a total of six male and 11 female specimens (= syntypes), of which six males and nine females were found during this study. Sinclair (1994) transferred this species to the genus *Trichoclinocera* after studying two male and two female syntype specimens borrowed from ZIN, but a lectotype was not designated by Sinclair (1994).

***Trichoclinocera tadjikistana* (Vaillant, 1960)**
(Fig. 19)

Seguyella tadjikistana Vaillant, 1960b: 184. Type locality (by lectotype designation): Dushanbe, Tajikistan.

Seguyella tadjikistana: Chvála & Wagner, 1989: 322 (catalogue).

Trichoclinocera tadjikistana (Vaillant): Sinclair, 1994: 1016 (new combination).

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled [printed in Cyrillic]: “Seguyella/ tadjikistana/ VAILLANT/ #m/ F. Vaillant dét. [yellow label]”; “Stalinabad [= Dushanbe]/ Tajik. [= Tajikistan] predgorja [= foothills], Goussakovsky 18.iv.[19]43,”; “Trichoclinocera/ tadjikistana/ Det. B.J. Sinclair 1993”; “LECTOTYPUS/ Seguyella/ tadjikistana Vaillant/ des. Sinclair, Shamshev, Gattolliat 2020 [red label]” (ZIN, INS_DIP_0000609). **PARALECTOTYPES: Tajikistan:** same data as lectotype (1 ♀, ZIN); Viskharvi on Pyandzh River, Tajikistan, 21.x.1942, Stackelberg (1 ♀, ZIN); Taval-dara, N slope of Darvazskiy Ridge, 7–11.x.1942, A.A. Stackelberg (1 ♂, 4 ♀♀, ZIN; ♂ examined and dissected by B.J. Sinclair); same data except, GBIFCH00606851 (Fig. 19) (1 ♂, MZLS, slide).

Remarks. Vaillant (1960b) designated Viskharvi as the type locality, which was represented by one male and one female specimen. Only the female specimen was

found and the male specimen appears to be lost. We have chosen a lectotype male from Dushanbe, which is some 200 km east of Viskharvi.

Sinclair (1994) transferred this species to the genus *Trichoclinocera* after studying two male and two female syntype specimens borrowed from ZIN, but did not designate a lectotype.

***Wiedemannia bicolorata* Vaillant, 1960**
(Fig. 20)

Wiedemannia (*Chamaedipsia*) *bicolorata* Vaillant, 1960b: 175. Type locality (by lectotype designation): Kondara Canyon, valley of Varzob River, Tajikistan.

Wiedemannia (*Chamaedipsia*) *bicolorata*: Chvála & Wagner, 1989: 325 (catalogue); Sinclair, 1995: 713.

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled [printed in Cyrillic]: “Wiedemannia/ (Chamaedipsia)/ bicolorata/ VAILLANT/ ♂/ F. Vaillant dét. [yellow label]”; “usch. [=uschelje, canyon] Kondara, dol./ r. [= dolina reki, valley of river] Varzob, Taj. [= Tajikistan]/ Stackelberg 7.xi.[1]944”; “LECTOTYPUS/ Wiedemannia (Chamaedipsia)/ bicolorata Vaillant/ des. Sinclair, Shamshev, Gattolliat 2020 [red label]” (ZIN, INS_DIP_0000610). **PARALECTOTYPES: Tajikistan:** same data as lectotype (1 ♂, 3 ♀♀, ZIN; including 1 ♂ and 1 ♀ on one pin); Rakhaty, Gissarskaya valley, 5.viii.1943, Stackelberg (3 ♀♀, ZIN, pinned); Taval-dara, N slope of Darvazskiy Ridge, 7.x.1942, Stackelberg (1 ♂, ZIN, pinned); Viskharvi on Pyandzh River, 21.x.1942, A.A. Stackelberg, GBIFCH00606843 (1 ♂; MZLA, slide); same data except, GBIFCH00606844 (1 ♂, MZLS, slide); same data except, GBIFCH00654930 (1 ♂, MZLS, pinned); Kovron, near Kalay-khumb, 20.x.1942, A.A. Stackelberg, GBIFCH00654929 (1 ♀, MZLS, pinned; 1 ♀, ZIN).

Remarks. Vaillant (1960b) designated “Canon de Kondara” as type locality and he studied three males and four females, of which two male and three female specimens were found during this study. Several pairs of facial setae are present on a number of specimens.

***Wiedemannia fallaciosa* (Loew, 1873)**

Clinocera fallaciosa Loew, 1873: 44. Type locality: “Pannoniä inferiori et in confinibus Daciae regionibus (Kowarz)” ex titulo [Herculesbad, Romania].

Material examined. Kazakhstan: Alma-Ata, Pogan-ka River, on stones, 8–24.viii.1942, A.A. Stackelberg (3 ♂♂, 1 ♀, ZIN). **Tajikistan:** Taval-dara, N slope of Darvazskiy Ridge, 7 and 9.x.1942, A.A. Stackelberg (2 ♀♀, MZLS; 13 ♂♂, 12 ♀♀, ZIN); Kalai-khumb, Darvaz, 21.viii.1943, A.A. Stackelberg (2 ♂♂, MZLS; 4 ♀♀,

ZIN); Stalinabad [=Dushanbe], foothills, 18.iv.1943, V.V. Gussakovskij (1 ♂, MZLS).

Remarks. Some pinned specimens (MZLS) were found partially destroyed by dermestids.

***Wiedemannia foliacea* Vaillant, 1960**

(Fig. 21)

Wiedemannia (Chamaedipsia) foliacea Vaillant, 1960b: 176. Type locality (by lectotype designation): Dushanbe, valley of Dushanbinka River, Tajikistan.

Wiedemannia (Chamaedipsia) foliacea: Chvála & Wagner, 1989: 325 (catalogue); Sinclair, 1995: 714.

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled [printed in Cyrillic] [Tajikistan]: “Wiedemannia/ (Chamaedipsia)/ foliacea/ VAILLANT/ ♂/ F. Vaillant dét. [yellow label]”; “Stalinabad [now Dushanbe],/ dol. [=dolina, valley]/ Dyushambinka [=Dushanbinka, a river]/ Stackelberg 13.v.[19]43”; “LECTOTYPUS/ Wiedemannia (Chamaedipsia)/ foliacea Vaillant/ des. Sinclair, Shamshev, Gattolliat 2020 [red label] (ZIN, INS_DIP_0000611). **PARALECTOTYPES:** **Tajikistan:** same data as lectotype, GBIFCH00606845 [incorrectly interpreted as “Vallée du ruisseau Goulbista”] (1 ♂, MZLS, slide); same data as lectotype, GBIFCH00654932 (1 ♂, MZLS, pinned); same data as lectotype (1 ♂, 2 ♀♀, ZIN, pinned); Stalinabad [=Dushanbe], foothills, 18.iv.1943, V.V. Goussakovskij (2 ♀♀, ZIN); Stalinabad [=Dushanbe], foothills, 27.vii.1945, V.V.

Goussakovskij, GBIFCH00606846 (1 ♂, MZLS, slide); Viskharvi on Pyandzh River, 21.x.1942, A.A. Stackelberg, GBIFCH00654931 (1 ♀, MZLS, pinned).

Additional material examined. Tajikistan: Stalinabad [=Dushanbe], Botanical garden, 13.v.1943, Stackelberg (1 ♀, ZIN).

Remarks. Vaillant (1960b) did not designate a type specimen for this species. Vaillant (1960b) listed a total of seven male and five female syntypes, of which five males and five females were found for this study. Additional material of this species has been identified in ZIN, which was not included in the original loan to Vaillant.

***Wiedemannia lota* Walker, 1851**

Wiedemannia lota Walker, 1851: 107. Type locality: Wicklow County, Ireland.

Atalanta (Philolutra) astigmatica Stackelberg, 1937: 123. Type locality: “Kara-Kala” (= Magtymguly, 38°26'N 56°18'E), Turkmenistan.

Atalanta astigmatica: Sinclair & Shamshev, 2019: 163 (lectotype designation, new synonym).

Material examined. Turkmenistan: Kara-kala [now Magtymguly], Syumy, viii.1931, P.A. Petristsheva (1 ♂, MZLS; Sinclair & Shamshev 2019, fig. 3), ix.1931 (2 ♂♂, ZIN (Sinclair & Shamshev 2019, figs 1, 2), 1 ♂, MZLS). **Tajikistan:** Stalinabad [=Dushanbe], valley of Gulbista River, 20.iv.1943, A.A. Stackelberg (1 ♂, ZIN; 1 ♂, on slide GBIFCH00606855, 1 ♀, MZLS); Stalinabad [=Du-



Figs 20–22. Specimens from Vaillant (1960b). **20.** *Wiedemannia bicolorata* Vaillant, two paralectotype slides. **21.** *Wiedemannia foliacea* Vaillant, two paralectotype slides. **22.** *Wiedemannia similis* Vaillant, lectotype slide.

shanbe], foothills, 18.iv.1943, V.V. Gussakovskij (1 ♀, MZLS); Rakhaty, Gissarskaya valley, 5.viii.1943 (1 ♀, ZIN); Taval-dara, N slope of Darvazskiy Ridge, 7.x.1942, A.A. Stackelberg (2 ♀♀, ZIN).

Additional material examined. Tajikistan: Stalinabad [=Dushanbe], valley of river Dyushambinka [=Dushanbinka], 13.v.1943, Stackelberg (2 ♂♂, ZIN); Stalinabad [=Dushanbe], valley of river Gulbista, 20.iv.1943, Stackelberg (1 ♂, ZIN).

Remarks. The specimens from Turkmenistan were discovered to be the type specimens for *Atalanta astigmatica* Stackelberg (Sinclair & Shamshev 2019).

***Wiedemannia similis* Vaillant, 1960**
(Fig. 22)

Wiedemannia (Wiedemannia) similis Vaillant, 1960b: 178. Type locality (by lectotype designation): Viskharvi, River Pyandzh, Tajikistan.

Wiedemannia (Wiedemannia) similis: Chvála & Wagner, 1989: 324 (catalogue); Sinclair, 1995: 716.

Type material examined. LECTOTYPE (here designated in order to fix identity of the species), ♂ labelled (Fig. 22) [printed in Cyrillic] [Tajikistan]: “Viskharvi on r. [=reka, river]/ Pyandzh, Taj. [=Tajikistan]/ 21.x.[1]942, Stackelberg”; “LECTOTYPE/ *Wiedemannia/ (Wiedemannia) similis/* Vaillant, 1960/ des. Sinclair, Shamshev,/ Gattolliat 2020 [red label]”; “*Wiedemannia (Wiedemannia) similis* VAILLANT ♂/ Défilé de Viskharvi, Mas-sif/ de Darvaz, Tadzikistan./ 21.X.1942/ A.A. STACKELBERG coll./ F. VAILLANT”; “GBIFCH/ 00606847” (MZLS, slide). **PARALECTOTYPES: Tajikistan:** same data as lectotype (2 ♀♀, ZIN); Taval-dara, N slope of Darvazskiy Ridge, 9.x.1942, A.A. Stackelberg (2 ♀♀, ZIN).

Remarks. Vaillant (1960b) did not designate a type specimen for this species. He listed one male and five female syntypes, of which one male and four females were found during this study.

Acknowledgements. Christophe Daugeron (Paris Museum) is thanked for directing the search by BJS and IVS for the types of Vaillant to Lausanne. Jim O’Hara (Ottawa), Patrice Bouchard (Ottawa) and Neal Evenhuis (Honolulu) are thanked for discussions concerning type material status. Ian Quintas and Maud Liégeois (MZLS) greatly contributed to this study by inventorying and digitalizing the 1300 slides of the Empididae collection deposited by François Vaillant at MZLS. Alexey Kovalev helped to take photos in ZIN. The study of IVS was performed in the frames of the Russian State Research Project no.

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Research article

[urn:lsid:zoobank.org:pub:EA017B83-DD67-45CA-9555-6DB9D261A40D](https://zoobank.org/pub/EA017B83-DD67-45CA-9555-6DB9D261A40D)**Taxonomic revision of the Levant moles of Turkey
(Mammalia: Talpidae)****Haluk Kefelioğlu¹, Boris Kryštufek², Ahmet Yesari Selçuk³, Rainer Hutterer^{4,*} & Jonas J. Astrin⁵**^{1,3}Department of Biology, Faculty of Science, Ondokuz Mayıs University, Samsun, Turkey²Slovenian Museum of Natural History, Prešernova 20, SI-1000 Ljubljana, Slovenia^{4,5}Zoologisches Forschungsmuseum Alexander Koenig, Leibniz-Institut für Biodiversität der Tiere, Adenauerallee 160, D-53113 Bonn, Germany*Corresponding author: Email: R.Hutterer@leibniz-zfmk.de¹[urn:lsid:zoobank.org:author:592452AF-02D3-4DC3-A350-0DFCE829A3F5](https://zoobank.org/author/592452AF-02D3-4DC3-A350-0DFCE829A3F5)²[urn:lsid:zoobank.org:author:FB4835B1-618E-4A0E-8917-078A90328D97](https://zoobank.org/author/FB4835B1-618E-4A0E-8917-078A90328D97)³[urn:lsid:zoobank.org:author:2F906968-32C8-4359-AC96-76049F6E229B](https://zoobank.org/author/2F906968-32C8-4359-AC96-76049F6E229B)⁴[urn:lsid:zoobank.org:author:16023337-0832-4490-89A9-846AC3925DD8](https://zoobank.org/author/16023337-0832-4490-89A9-846AC3925DD8)⁵[urn:lsid:zoobank.org:author:50661540-FD30-4ABA-8415-6B3069105E93](https://zoobank.org/author/50661540-FD30-4ABA-8415-6B3069105E93)

Abstract. This paper examines the distribution and the morphological and genetic variation of *Talpa levantis*. Previous records from Thrace were re-identified as *Talpa martinorum*, restricting the range of *Talpa levantis* to northern Asia Minor and the Caucasus in Georgia, Armenia and Russia. Within *Talpa levantis*, we found three moderately distinct populations in western, central, and eastern Turkey. While the central one is *T. l. levantis* and the eastern one *T. l. transcaucasica*, the western subspecies had not been recognized before and is therefore named as a new subspecies.

Key words. Cytochrome *b*, molecular taxonomy, morphology, phylogeography, subspecies, *Talpa levantis*, *Talpa martinorum*.

INTRODUCTION

Mammalian systematics is dynamic and new species are continuously being recognized. The number of mammal species, estimated at 5,416 in 2005 (Wilson & Reeder 2005) increased to 6,495 just 13 years later (Burgin et al. 2018), an astonishing 20% increase. This progress was at least partly generated by a wide application of new research tools, above all the highly effective DNA-based methods which are capable of delimiting morphologically cryptic species (Baker & Bradley 2006).

Our focus in this study is the evolutionary divergence, taxonomy and species richness of the Eurasian mole genus *Talpa* Linnaeus, 1758 in Turkey. The genus is endemic to the western Palaearctic region and is well known to the lay public for its distinctive external appearance and the characteristic heaps of soil, mole-hills, which are abundant in temperate zone meadows. Less known to the public is the fact that species delimitation in *Talpa* has been progressing very slowly and continuing disagreements among experts over the number of species exist (Kryštufek & Motokawa 2018). Strong selective pressures for a semifossorial life blur the phylogenetic signal in morphological structures and convergences/

parallelisms are overwhelming. Traditional taxonomy therefore heavily underestimated the species richness of moles. The state of knowledge progressed only when the information in nucleotide sequences was combined with a wide taxonomic sampling (Bannikova et al. 2015). Between 2005 and 2020, the number of recognized species in the genus *Talpa* increased from nine (Hutterer 2005) to fourteen (Kryštufek & Motokawa 2018, Kryštufek et al. 2018a, Demirtaş et al. 2020), an increase of 56%.

Bannikova et al. (2015) pointed out several unresolved taxonomic problems, which required further attention. One of these problems concerns the Levant mole *Talpa levantis* Thomas, 1906, which displays a very high intra-specific genetic divergence. Earlier on, the Levant mole was thought to range from the south-eastern Balkans across northern Turkey into the Caucasus and the Caspian coast of Iran. It was subsequently shown that the western-most populations represent a species new to science (*Talpa martinorum* Kryštufek et al. 2018), that those from the Caspian coast are identical with *T. talyschensis* Vereschagin, 1945, and that the rest can be split into the western *T. levantis* proper, and the eastern *T. transcaucasica* Dahl, 1945 (Demirtaş et al. 2020). In this paper we are re-addressing the geographical variability of Levant

moles occupying Turkey by combining, for the first time, molecular evidence with morphological data. Our aim was to gain a more holistic view on the taxonomic structure of the Levant mole.

MATERIAL & METHODS

Specimens. We studied small blind moles from throughout Turkey (Fig. 1, Appendix I) which were earlier classified as *T. levantis*. The European material was taken into consideration because it had so far not been screened genetically and because Demirtaş et al. (2020) suggested these populations to be conspecific to those occupying Anatolia.

Tissue samples for DNA analysis were placed in non-denaturated 96% ethanol and subsequently refrigerated. The cytochrome *b* (*Cyt b*) gene was sequenced for 20 Levant moles and these new sequences were analyzed together with 17 additional Levant mole sequences from Turkey and the Caucasus region. Furthermore, we downloaded from the GenBank database 23 sequences of 10 *Talpa* species, and an outgroup Talpinae sequence (*Urotrichus talpoides*). Collecting data associated with the new sequences and all GenBank numbers for Levant moles are given in Table 1 [sequences submitted to GenBank]; for the remaining GenBank numbers see Table 1.

Specimen vouchers (skins and skulls) are deposited in the following collections (acronyms in parentheses): National Museum of Natural History, Washington D. C.

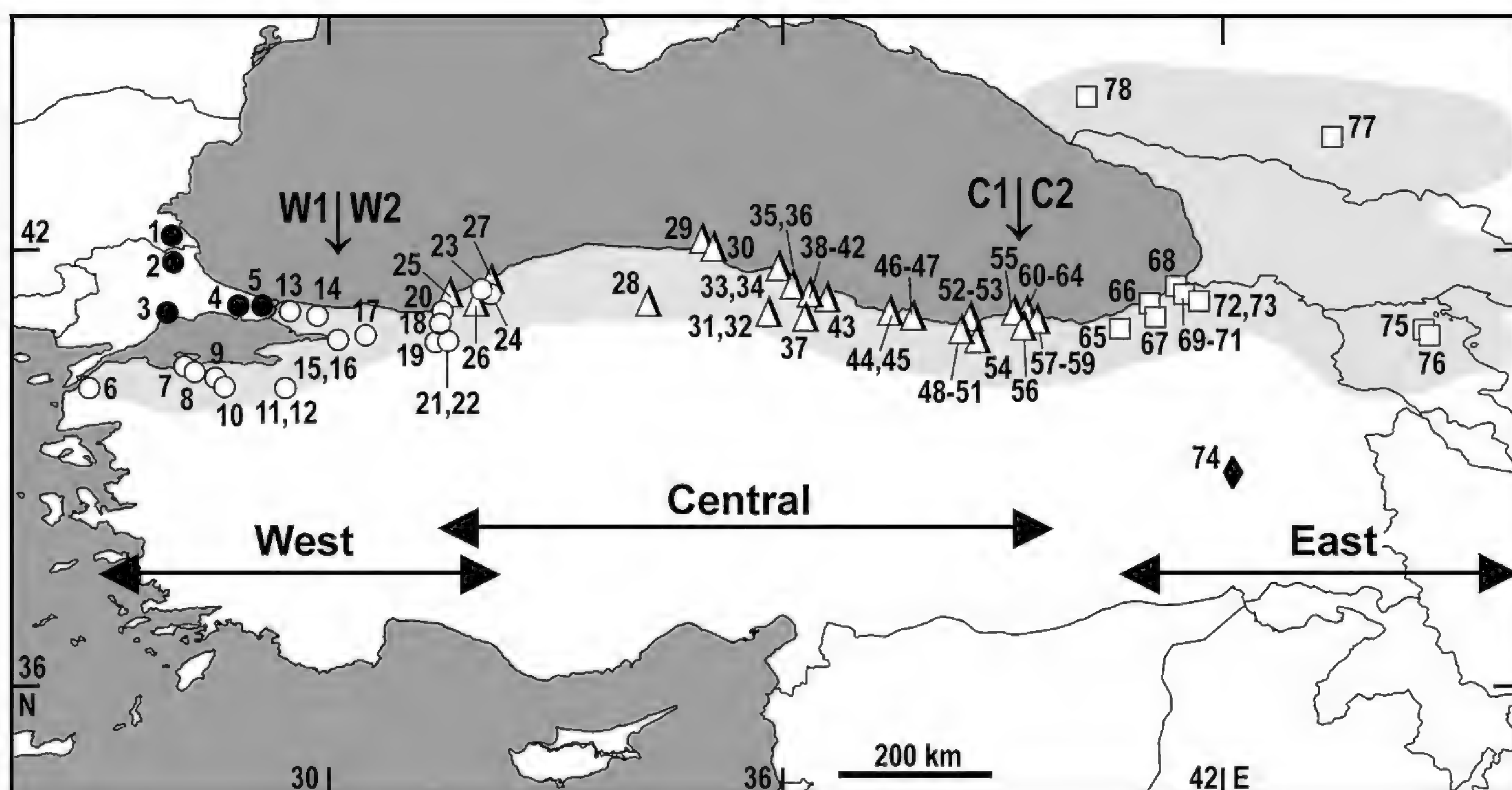


Fig. 1. Sample locations of *Talpa levantis* and *T. martinorum*. Symbols: ○ *Talpa levantis dogramacii* ssp. nov.; △ *T. levantis levantis*; □ *T. l. transcaucasica*; ◆ *T. levantis* ssp.; ● *T. martinorum*. Symbols correspond to those in Fig. 1 and Table 1. Tentative range of *Talpa levantis* is shaded grey and tentative longitudinal ranges of lineages are shown by left-right arrows. Downwards arrows show contact points between the sublineages of Western (W1, W2) and Central (C1, C2) lineages. Population near Lake Van (pt. 74) is presumably an isolate of unknown genetic identity, known from a single locality. Bulgaria: 1–Kondolovo. Turkey: 2–Kırklareli, Dupnisa; 3–Tekirdağ, Çorlu; 4–İstanbul, Çatalca; 5–İstanbul, Bahçeköy, Belgrad Ormanı; 6–Çanakkale; 7–Kapıdağ, Balıkesir; 8–Balıkesir, Manyas; 9–Balıkesir, Bandırma; 10–Bursa, Karacabey; 11–Bursa, Uludağ; 12–Bursa, Kirazlıyayla, Uludağ; 13–İstanbul, Mahmutşevketpaşa; 14–İstanbul, Şile; 15–İzmit; 16–İzmit, Kandıra; 17–Adapazarı, Kazımpaşa, Alandüzü köyü; 18–Düzce; 19–Bolu, Abant; 20–Kocaman forestry, half was between Akçakoca and Alaplı; 21–Bolu, Seben; 22–Bolu, Karadere; 23–Zonguldak, Uzungüney Köyü; 24–Zonguldak, Çaycuma; 25–Zonguldak, Alaplı; 26–between Zonguldak and Bolu; 27–Zonguldak, between Sefercik and Filyos; 28–Tosya, Kastamonu; 29–Sinop, Abalı Köyü; 30–Sinop, Gerze; 31–Amasya; 32–Amasya, Tatlıcak köyü; 33–Samsun, Bafra; 34–Samsun, Kızılırmak delta, Bafra; 35–Samsun, Erikli Köyü; 36–Samsun, Ondokuzmayıs, Derneköy; 37–Taşova District, Borabay Lake; 38–Samsun, Karakavuk; 39–Samsun, İncesu Köyü; 40–Samsun; 41–Samsun, Kurupelit; 42–Samsun, Tekkeköy; 43–Samsun, 3 km south Çarşamba; 44–Ordu, Fatsa; 45–Ordu, Fatsa, Geyikçeli Köyü; 46–Ordu, Ulubey; 47–Ordu; 48–Giresun, Yavuzkema; 49–Giresun, Batlama Deresi; 50–Giresun, Kümbet; 51–Giresun, Dereli; 52–Giresun; 53–Giresun, Ülper; 54–Trabzon, Mereyem Ana; 55–Giresun, Görele; 56–Ordu, Torul, Gümüşhane; 57–Trabzon, Maçka; 58–Trabzon, Maçka, Altındere; 59–Trabzon, Maçka, Sümela Manastırı; 60–Trabzon; 61–Trabzon, Khotz; 62–Trabzon, Özdil; 63–Trabzon, Oymaltepe; 64–Trabzon, Yomra; 65–Rize, Ovit, Ovit Yaylası; 66–Rize, Ardeşen; 67–Ayder, İlicasi; 68–Artvin, Hopa, Sugörenköyü; 69–Artvin, Hopa 8 km east; 70–Artvin; 71–Artvin, Ardanuç; 72–Artvin, Yalnızcamgeçidi; 73–Ardahan, Çam Geçidi; 74–Bitlis, Tatvan, Lake Van. Armenia: 75–Margahovit; 76–Fioletovo. Russia: 77–Kabardino-Balkaria, Nalchik; 78–Adygea.

Table 1. Details of sample localities (mapped in Figure 1) for Levant moles s. lat. and cytochrome *b* haplotypes found within them.

Location No.	Country	Locality	Haplo-type	Voucher No.	GenBank Acc. No. (bold = new)	References
● <i>T. martinorum</i>						
1	Turkey	Kırklareli, Dupnisa	TR13		MT738563	This study
2	Bulgaria	Mt. Strandzha, Kondolovo		ZFMK-MAM-2017.1151	MH093595	Kryštufek et al. 2018a
4	Turkey	İstanbul, Çatalca	TR15		MT738565	This study
○ <i>T. levantis</i> West						
7	Turkey	Kapıdağ, Balıkeşir	TR18	OMU 1346	MT738568	This study
11		Bursa, Uludağ	TR6	OMU 1350	MT738556	This study
			TR7	OMU 1352	MT738557	This study
			TR8	OMU 1353	MT738558	This study
				PMS 10650	FN640571	Colangelo et al. 2010
23		Zonguldak, Uzungüney Köyü			KP717336	Bannikova et al. 2015
25		Düzce	TR16	OMU 1344	MT738566	This study
			TR17	OMU 1345	MT738567	This study
29		Zonguldak, Çaycuma			KP717338	Bannikova et al. 2015
△ <i>T. levantis</i> Central						
20		Zonguldak, Alaplı			KP717340	Bannikova et al. 2015
26		Bolu-Zonguldak	TR19	OMU 1343	MT738569	This study
28		Zonguldak, Sefercik – Filyos			KP717339	Bannikova et al. 2015
					KP717343	Bannikova et al. 2015
33		Amasya	TR14		MT738564	This study
42		Samsun	TR11		MT738561	This study
				PMS 10299	FN640572	Colangelo et al. 2010
46		Ordu, Fatsa	TR9		MT738559	This study
49		Ordu	TR20		MT738570	This study
			TR12		MT738562	This study
51		Giresun	TR10	OMU 1349	MT738560	This study
52		Giresun, Ülper	TR20	OMU 1340	MT738552	This study
53		Giresun, Kümbet	TR5		MT738555	This study
59		Trabzon, Maçka	TR1	OMU 1354	MT738551	This study
64		Trabzon, Özdil	TR4	OMU 1351	MT738554	This study
65		Trabzon, Oymaltepe	TR3	OMU 1347	MT738553	This study
□ <i>T. levantis</i> East						
76	Turkey	Ardahan, Cam Geçidi		PMS 21658	FN640570	Colangelo et al. 2010
77	Armenia	Margahovit			KP717335	Bannikova et al. 2015
78		Fioletovo			KP717337	Bannikova et al. 2015
					KP717342	Bannikova et al. 2015
79	Russia	Kabardino-Balkaria, Nalchik			KP717334	Bannikova et al. 2015
					KP717341	Bannikova et al. 2015
		Kabardino-Balkaria			FN640573	Colangelo et al. 2010
					FN640574	Colangelo et al. 2010
80	Russia	Adygea			KP717344	Bannikova et al. 2015
					KP717345	Bannikova et al. 2015
					KP717346	Bannikova et al. 2015

drial Cytochrome *b* (Cyt *b*) gene, we used the Qiagen Multiplex PCR kit, following the manufacturer's specifications and based on 2 µl undiluted DNA template in 20 µl total reaction volumes. DNA fragments of 1043 bp were amplified with an Applied Biosystems GeneAmp PCR System 2700 (Life Technologies), applying the primers L14724ag (5'-ATGATATGAAAAACCATC-GTTG-3') and H15915ag (5'-TTTCCNTTTCTG-GTTTACAAGAC-3'; Guillén-Servent & Francis 2006). PCR routine followed a 'touch-down' protocol: Taq activation: 15 min at 95°C; first cycle set (15 repeats): 35 s denaturation at 94°C, 90 s annealing at 60°C (-1°C per cycle) and 90 s extension at 72°C. Second cycle set (25 repeats): 35 s denaturation at 94°C, 90 s annealing at 50°C, and 90 s extension at 72°C.

After enzymatic clean-up, all PCR products were Sanger-sequenced at Macrogen, Europe's commercial Sanger sequencing service (Amsterdam, NL). Sequences were assembled, inspected and aligned using Geneious vers. R7 (Biomatters, Auckland, New Zealand).

Bayesian analyses were conducted using MrBayes vers. 3.2 (Ronquist & Huelsenbeck 2003). Specific parameters for a GTR+G model were equated by the program. GTR+G is a typical substitution model that includes sufficient degrees of freedom and factors in heterogeneity of substitution rates among sites, but avoids overparameterization as potentially induced by modelling invariable sites (Jia et al. 2014 showed the irrelevance of including invariable site assumptions in datasets below species level). Parameters were unlinked between the 3rd versus 1st plus 2nd codon positions, based on the fact that third codon 'wobble' positions are less influenced by selective pressure and much less conserved than 1st and 2nd positions, hence requiring separate parameter calculation. MrBayes was run for 20 million generations and using the default number of chains. Every 1000th tree was sampled. Negative log-likelihood score stabilization was determined in a separate visualization. Accordingly, we retained 39,960 trees, which were used for building a 50%-majority rule consensus tree with posterior probabilities (Fig. 2).

Morphological analyses. Our study was based on visual examination of museum specimens, both macroscopically and under a stereomicroscope at different magnifications. Skull morphology was quantified by means of five cranial variables, which were scored using a Vernier calliper with accuracy to the nearest 0.1 mm (acronyms in parentheses): condylobasal length of skull (CbL), length of maxillary tooth-row (MxT; canine to 3rd molar), breadth of braincase (BcB), breadth of rostrum over canines (RoC), and breadth of rostrum over molars (RoM). The length of the posterior part of braincase was measured on printed skull photographs. External measurements were obtained from specimen tags: body mass (BWt), length of head and body (H&B), length of tail (TL), and length

of hind foot (HfL). Body mass is given in grams and the remaining measurements in millimetres.

Based on molecular results, the specimens were grouped into three operational taxonomic groups (OTUs), which were essentially identical to phylogenetic lineages. Because molecular characters were not known for all museum specimens, we presumed that the lineages are allopatric and classified skulls on this basis. Specimens from the zone of overlap between the Western and the Central lineages were excluded, while specimens from the little-known contact zone between the Central and the Eastern lineages were assigned to the group using classification criteria derived from a discriminant function analysis based on securely identified vouchers. We used the same labels for denomination of phylogenetic lineages and morphological OTUs (Western, Central and Eastern). Moles from Lake Van (pt. 74 in Fig. 1) are traditionally classified as *T. levantis* although they are an isolate with unknown molecular identity. We used morphometric analysis to compare this sample with the three OTUs of *T. levantis*.

Heterogeneity between OTUs was evaluated in one-way or two-way analyses of variance (Anova). To characterize the craniometric variation among samples and to find patterns in our high-dimensional data, we performed a principal components analysis (PCA) and a discriminant function analysis (DFA) on log₁₀-transformed cranial variables. Rates of correct classification of *a priori* defined species were evaluated in a discriminant analysis. To evaluate the performance of the DFA and avoid the risk of overfitting the data, all analyses were cross-validated using the jack-knife procedure, in which each specimen is classified into a group using the discriminant function derived from all specimens except the specimen being classified. Relative length of maxillary tooth row (MxT%) and relative breadth of rostrum over molars (RoM%) were expressed as quotients with the condylobasal length of skull and multiplied by 100. Because of undesirable statistical properties of ratios, we did not use them in multivariate analyses. Statistical tests were run in Statistica 7.0 (StatSoft Inc., OK, USA) and SPSS Statistics 2012 (IBM Analytics, NY).

RESULTS

Molecular results. Sequencing of the new Turkish samples resulted in 19 haplotypes of the length 1043 bp (one sequence missing one base, another three). A further sequence that showed a clear (and accordingly trimmed) read for only 403 bp was integrated in the dataset (sample TR09 from Fatsa Ordu). Overall, the dataset included 6 ambiguous positions in individual sequences (see attached alignment in Appendix II).

In the Bayesian tree (Fig. 2), haplotypes clustered according to the earlier results of Bannikova et al. (2015),

although tree topologies differed in some minor respects. Moderate nodal supports prevent us from discussing the deeper branching topology (outside *T. levantis*) in detail. Turkish samples grouped into four clusters. The only two haplotypes from European Turkey (TR13, TR15) aligned with the reference sequence of *T. martinorum* from Bulgaria. Levant mole haplotypes grouped into three lineages, which showed strong geographic associations and were designated as the Western, Central and Eastern lineage. The Eastern lineage holds a moderately supported basal position with regard to the Western and Central lineages. The collecting sites of specimens associated genetically with the Central and Eastern lineages were separated by a distance of about 225 km, without any genetically screened samples in-between. On the other hand, the ranges of the Western and Central lineages overlapped to the east of the city of Zonguldak for a distance of at least 30 km in west-to-east direction. Besides this, the Western and Central lineages were further sub-structured, each into two allopatric sub-lineages. In

the Western lineage, the sublineages W1 and W2 were tentatively delimited by Sakarya, while the sub-lineages C1 and C2 of the Central lineage had a contact between Rize and Trabzon. The C2 sublineage occupies the majority of the range of Levant moles in Turkey by stretching along the Black Sea coast in west-to-east direction for ca. 650 km.

Within the Levant moles of Anatolia, the Cyt *b* divergence was highest between the Eastern and the Central lineages (highest pairwise *p*-distance at 8.0%), and amounted to 5.9% between the Central and the Western lineages. Genetic variation within the lineages was highest in the Central lineage (mean *p*-distance of 2.0%, highest pair-wise *p*-distance 3.4%), closely followed by the Western lineage (mean 1.7%, highest 2.9%), and was lowest in the Western lineage (mean 1.0%, highest 2.6%). In our dataset, the lowest *p*-distance among lineages was between the Central and Western lineages, with 3.5%.

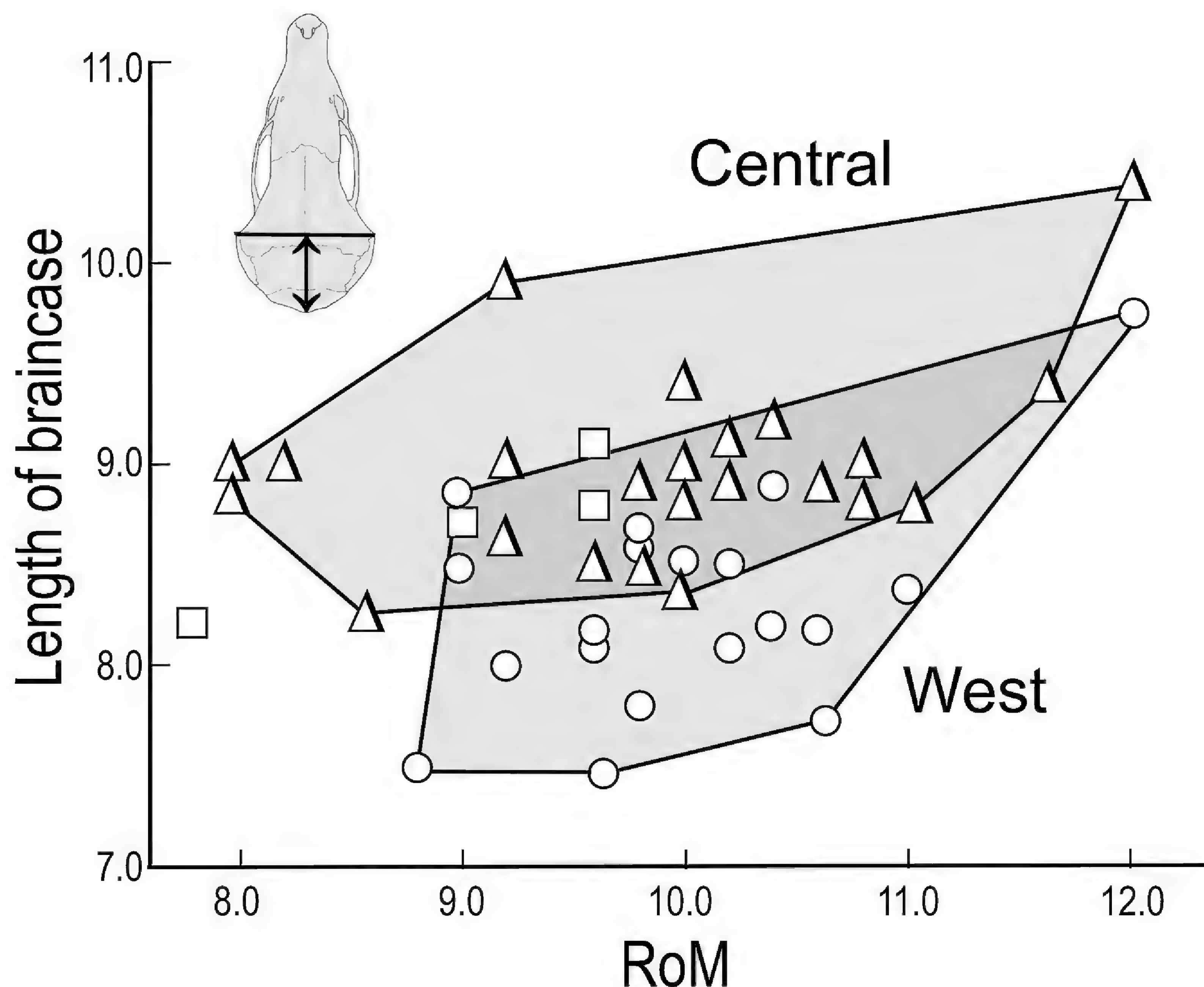


Fig. 3. Bivariate plot of length of neurocranium (see the left upper inset) against breadth of rostrum across molars (RoM) for three operational taxonomic units of *Talpa levantis*. Symbols are same as in Fig. 1.

Morphology. Moles from Turkish Thrace lack the parastyle on the anterior upper molars and were therefore classified as *T. martinorum* (cf. Kryštufek et al. 2018a). The parastyle is present in the majority of Anatolian individuals, as long as their molars are still comparatively unworn. Visual examination of skulls retrieved no quantitative cranial or dental traits among the *T. levantis* OTUs.

In the results of a two-way Anova, the major source of morphometric variation was the OTU and not the sexual category (Table 2). Therefore, five variables (H&B, HfL, CbL, MxT, RoM) showed significant heterogeneity among the OTUs and only three traits (BWt, H&B, BcB) were also sexually dimorphic. With the exception of the length of tail, there was no interaction between these two factors. Out of 27 pairwise comparisons, only ten showed significant differences in the Fisher LSD test. Six of them fell between the Central and Eastern OTUs, while two comparisons were significant between the Western and Central OTUs, and further two between the Western and Eastern OTUs, respectively. Males were more prone to the heterogeneity among OTUs (7 significant pairwise comparisons) than females (3 significant comparisons). The two quotients (MxT% and RoM%) showed a similar pattern as the linear measurements (Table 2).

When inspecting skulls macroscopically, we spotted slight differences in their shape and proportion. Therefore, in the Western OTU, the posterior outline of the braincase was less bowed than in the Central OTU, the overlap however was considerable (Fig. 3). Furthermore, the relative length of the maxillary tooth-row (MxT%) and the width of rostrum across molars (RoM%) showed a steady increase from the Eastern OTU to the Western OTU; the Central OTU was intermediate in both cases. Again, the overlap among the OTUs was sizeable (Fig. 4). We therefore tested our data set for possible longitudinal trends. Two external traits (BWt, TL), three craniodental variables (MxT, RoC, RoM) and both quotients (MxT% and RoM%) showed significant trends of a west-to-east decline (Table S1). The remaining traits (H&B, HfL, CbL, BcB) showed extremely low F-values ($F < 0.30$, $p > 0.59$). Moles in the west were therefore the heaviest, with longer tails, absolutely and relatively longer maxillary tooth-rows, relatively and absolutely broader rostra and less bowed posterior braincases. The eastern moles showed the lowest values for all these indices, while geographically intermediate moles were also transitional in these traits.

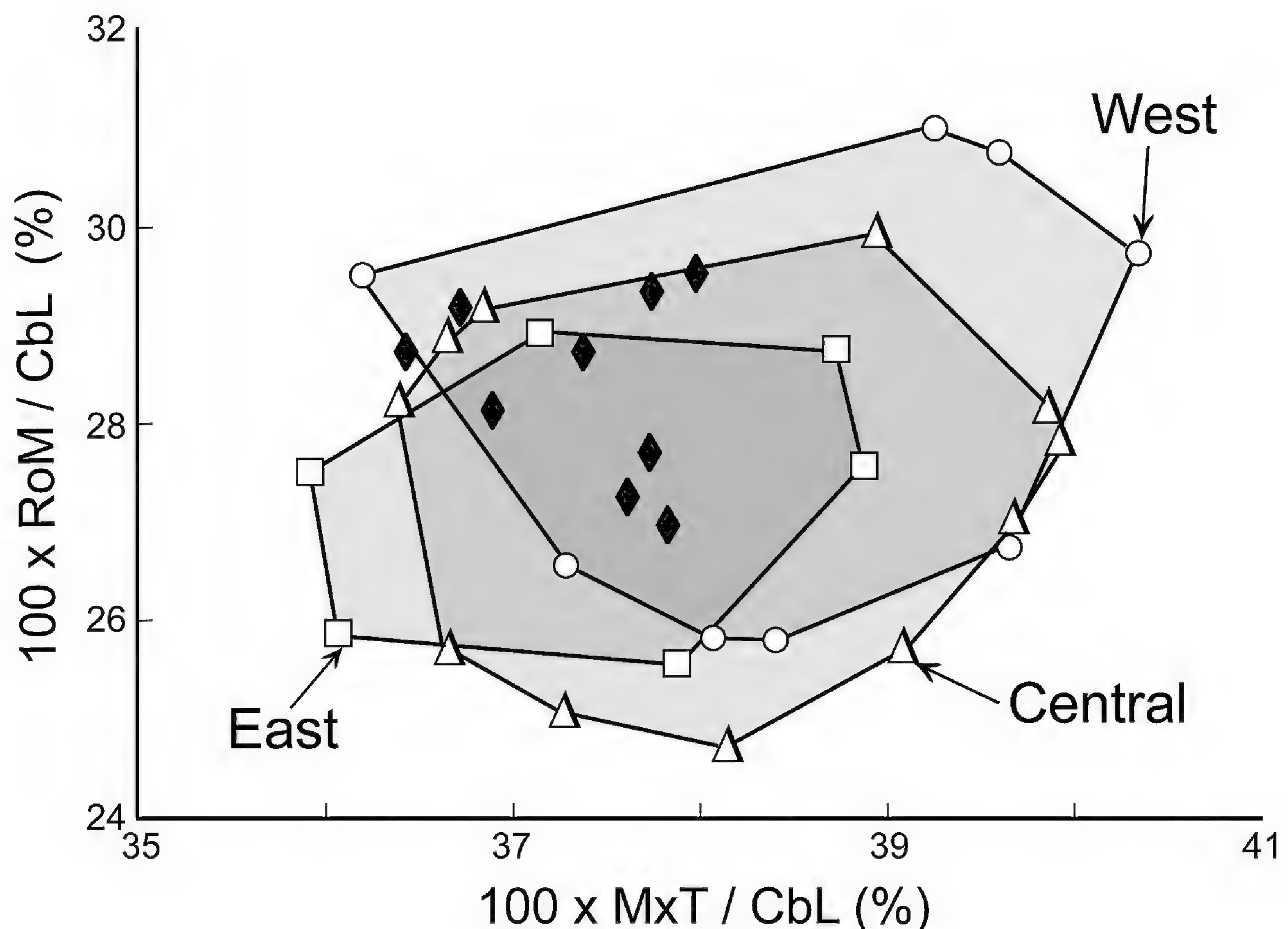


Fig. 4. Bivariate plot of breadth of rostrum across molars (RoM) against length of maxillary tooth-row (MxT), both expressed as quotients of the condylobasal length of skull and multiplied by 100, for three operational taxonomic units of *Talpa levantis* and the sample from Lake Van. Symbols are same as in Fig. 1.

Table 2. Descriptive statistics (mean and standard error) for three operational taxonomic units (OTUs) of *Talpa levantis*. Results of two-way Anova (sex and OTU as factors) and Fisher LSD test between the OTUs (W–Western; C–Central; E–Eastern) are shown in four columns on the right-hand side.

Trait		West			Central			East			Two-Way Anova		Scheffé test	
		N	Mean	SE	N	Mean	SE	N	Mean	SE		F-value	p	
BWt	males	26	54.88	1.448	25	55.32	1.477	6	51.25	3.014	OTU	1.18	0.311	
	females	13	52.00	2.048	29	47.63	1.371	7	49.14	2.791	Sex	5.90	0.017	
											Interaction	1.47	0.236	
H&B	males	29	122.41	1.244	34	126.09	1.149	14	121.57	1.791	OTU	4.27	0.015	W-C, C-E
	females	13	119.54	1.859	29	122.10	1.244	10	118.50	2.119	Sex	6.33	0.013	
											Interaction	0.09	0.912	
TL	males	29	27.90	0.469	34	27.32	0.433	14	28.00	0.675	OTU	2.37	0.098	
	females	13	28.62	0.700	29	28.31	0.469	9	25.56	0.842	Sex	0.24	0.626	
											Interaction	3.94	0.022	
HfL	males	29	18.76	0.245	34	19.12	0.227	14	17.94	0.354	OTU	3.93	0.022	C-E
	females	13	18.54	0.366	29	19.00	0.246	10	18.42	0.418	Sex	0.03	0.861	
											Interaction	0.58	0.563	
CbL	males	29	31.15	0.229	32	31.76	0.218	14	30.63	0.330	OTU	11.68	0.00002	C-E
	females	13	30.44	0.343	27	31.35	0.238	9	29.64	0.412	Sex	7.96	0.006	W-C, C-E
											Interaction	0.49	0.62	
MxT	males	30	11.95	0.095	35	12.09	0.084	14	11.51	0.133	OTU	12.60	0.00001	W-E, C-E
	females	14	11.75	0.133	28	12.01	0.094	9	11.36	0.166	Sex	1.99	0.161	C-E
											Interaction	0.19	0.824	
BcB	males	29	15.25	0.089	33	15.46	0.083	14	15.29	0.128	OTU	2.40	0.091	
	females	13	14.96	0.133	29	15.17	0.089	9	15.02	0.160	Sex	8.70	0.004	
											Interaction	0.00	0.996	
RoC	males	30	4.61	0.181	35	4.23	0.168	14	3.96	0.265	OTU	1.03	0.361	
	females	14	4.14	0.265	28	4.23	0.188	9	4.04	0.331	Sex	0.45	0.504	
											Interaction	0.83	0.439	
RoM	males	30	8.83	0.097	35	8.60	0.089	14	8.31	0.141	OTU	4.31	0.016	W-E
	females	14	8.70	0.141	29	8.72	0.098	9	8.40	0.176	Sex	0.09	0.770	
											Interaction	0.74	0.481	
Quo-tiens														
MxT%	males	28	38.42	0.159	32	38.19	0.148	14	37.55	0.225	OTU	7.50	0.0007	W-E, C-E
	females	13	38.62	0.234	27	38.27	0.162	8	37.67	0.298	Sex	0.90	0.345	W-E
											Interaction	0.00	0.984	
RoM%	males	29	28.34	0.222	32	27.04	0.211	14	27.11	0.319	OTU	9.08	0.0002	W-C, W-E
	females	13	28.53	0.331	27	27.74	0.230	8	27.83	0.422	Sex	4.82	0.030	
											Interaction	0.59	0.556	

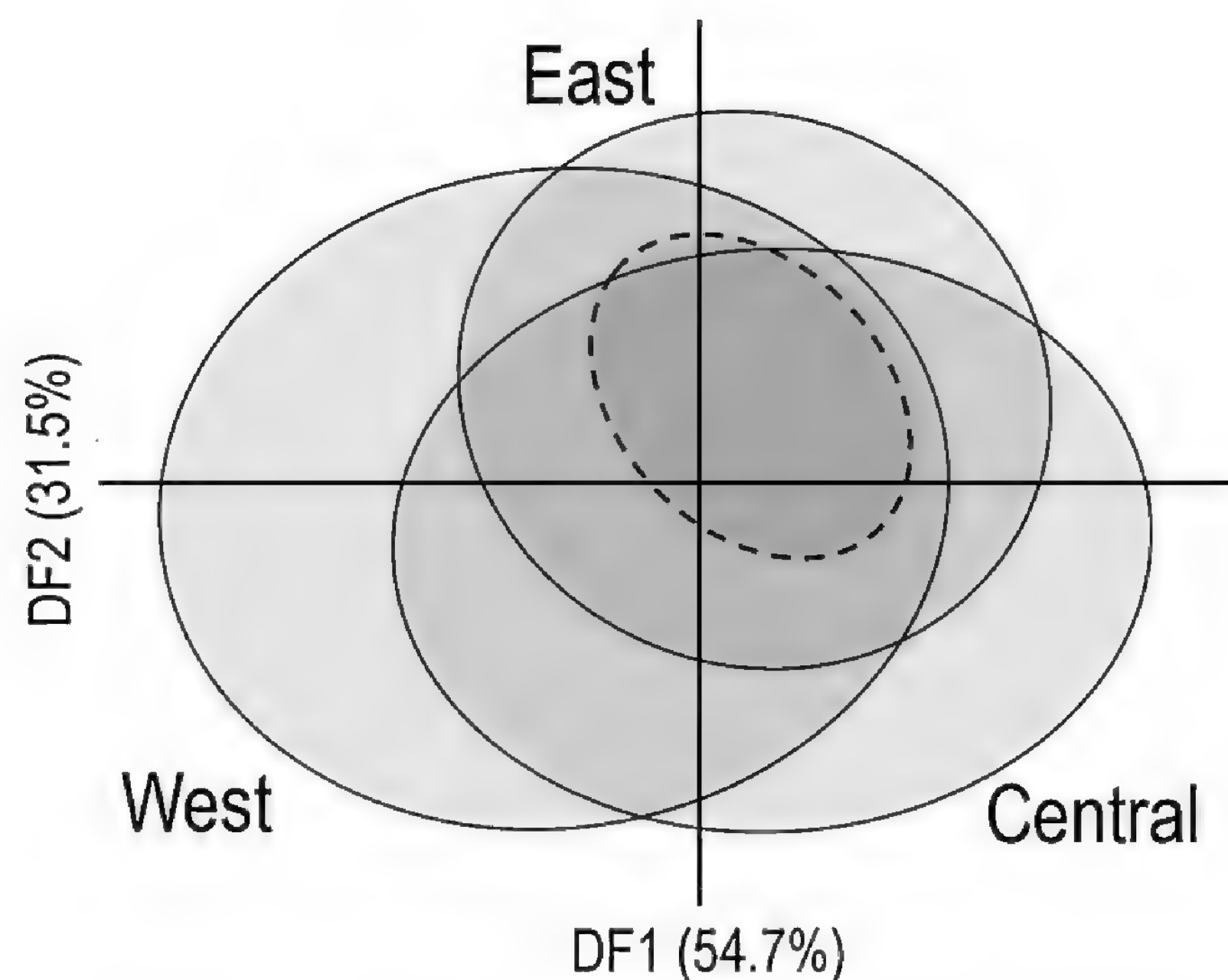


Fig. 5. The 95% confidence ellipses for dispersion of scores of four operational taxonomic units of *Talpa levantis* onto the first two discriminant axes derived from discriminant factor analyses of \log_{10} -transformed cranial variables. The proportion of variance explained by an axis is in parentheses. The ellipse for the Lake Van sample is shown by a dashed line.

The principal components analysis was run on a correlation matrix of all five cranial traits. One-way Anova retrieved significant heterogeneity among OTUs in four principal components (pc) out of a total of five. Quite remarkably, the highest F-values were by pc3 and pc5, i.e. two components which explained only a small proportion of variance (=10.4%) in the original data set (Table S2). Projection of specimen scores onto these components revealed a high overlap among OTUs and moles from Lake Van overlapped with all three OTUs (not shown).

Forward stepwise discriminant analysis on five cranial variables and with four groups (three OTUs and sample from Lake Van) as classification factor resulted in a moderately high Wilk's lambda ($=0.587$, $p<0.001$). All variables were included into the analysis, except for the braincase width ($F_{\text{to-enter}}=2.255$, $p=0.85$). Condylbasal length of the skull and maxillary tooth-row length had the highest $F_{\text{to-remove}}$ values (10.656 and 8.175, respectively; $p<0.00005$) and therefore contributed most to a discrimination between groups. Putting aside the Lake Van sample, the Mahalanobis squared distance (D^2) was high between the Western and the Eastern OTUs ($D^2=2.125$), moderate between the Western and the Central OTUs ($D^2=1.667$) and low between the Central and the Eastern OTU ($D^2=1.355$; all significant at $p<0.002$; $F>4.5$). The Lake Van sample was most similar to the Eastern sample ($D^2=1.690$, $p=0.046$), followed by the Central OTU ($D^2=2.006$, $p=0.006$) and the Western OTU ($D^2=2.759$, $p=0.001$). Predictability of classification was rather low and only 54.7% of cases were allocated into the actual group; this ranged from 80.0% of correct classifications for the Van sample, across 56.8% for the West-

ern OTU and 52.9% for the Eastern OTU, to 45.8% in the Eastern OTU. Cross-validation of classification with leave-one-out yielded very similar results with 52.0% of individuals being allocated to the actual group. The overlap between groups was therefore considerable and was evident also from the projection of specimen scores onto the first two discriminant axes, explaining 86.2% of variance in the original data set (Fig. 5). On the other hand, the cross-validation of classification results showed that we avoided the risk of overfitting data in our DFA. We therefore conclude that differences between the groups are slight but genuine.

DISCUSSION

Survival in Pleistocene refugia. There is a deep genealogical divergence among the three main Cyt *b* lineages of the Levant mole and such a pattern is a clear indication that these lineages originated from an allopatric fragmentation event (Avice 2000). The most ancient divergence in the Levant mole, which is between the Western + Central and the Eastern lineages, is estimated to have occurred at ca. 1.91 Mya (Demirtaş et al. 2020). The current phylogeographic pattern of the Levant mole is therefore clearly the legacy of climatic changes during the glacial-interglacial cycles of the Pleistocene when the newly emerged biogeographic barriers created by novel climatic conditions fragmented populations, prevented gene flow and triggered divergence in isolation.

Contrary to Europe where periodic expansion of ice sheets and the consequent cooling of temperatures profoundly impacted the survival of temperate biota throughout the Pleistocene (Hewitt 2000), the Quaternary environments in Anatolia were different in many respects. Glaciers persisted only at elevations above 2200 m (Erinç 1978) while the lowlands were affected by aridification (Webb & Bartlein 1992). In a highly diverse landscape of Anatolia, the endurance of temperate taxa was facilitated along the altitudinal gradient in a network of mountain refugia which provided moist conditions at intermediate elevations (Ansell et al. 2011). Fossorial moles are highly sensitive to soil humidity, which supports prey consisting primarily of earthworms (Kryštufek & Motokawa 2018). It is therefore feasible to presume that during the Pleistocene the progressing aridification pushed the Levant moles to higher elevations where they endured in humid enclaves. This fragmented the mole's range, just as an expansion of glaciers and tundra habitats repeatedly fragmented continuous distributions of numerous temperate taxa in Europe (Hewitt 2000). A combination of Anatolian topography and climatic history may have promoted a long-term local survival of the Levant mole in the Black-Sea (Pontic) Mountains, and simultaneously facilitated the independent evolutionary divergence of vicariant populations. At least five refugia can be deduced from

the topology of Cyt *b* trees (Demirtaş et al. 2020, and this study), which matches a spatially explicit picture of a wider pattern of endemism in Anatolia (e.g., Roces-Díaz et al. 2018). The Marmara region, which emerged in our study as an important refugial area for the Western lineage, has been identified by mammalogists as part of a permeable corridor for faunal exchanges between Europe and south-western Asia (Hosey 1982) but was never considered as being of particular importance for mammalian endemism.

The phylogeographic structuring of the Levant mole cannot be attributed to the external barriers. Demirtaş et al. (2020) stressed this for the Eastern part of the Pontic Mts. where no obvious obstacles separate the Central and the Eastern lineages. The situation is even more puzzling on the western end of the range where the Central haplotypes are parapatric with the Western ones.

Demirtaş et al. (2020) suggested for the Levant mole to occupy both sides of the Marmara and Bosphorus (also called the Turkish) straits. The idea of the intermittent continental bridge at the Turkish strait dates back to times of classical zoogeography (Kosswig 1955, Hosey 1982). As confirmed by recent phylogeographic studies, mammals crossed the Turkish straits moving from Europe to Anatolia (e.g., *Glis glis*; Helvacı et al. 2012), from Anatolia to Europe (e.g., *Microtus hartingi*; Kryštufek et al. 2018b) or in both directions (e.g., *Crocidura leucodon*; Dubey et al. 2007). The Levant mole, however, was obviously not such a transcontinental migrant. As already suggested by Kryštufek et al. (2018a) and confirmed in this study, the small blind moles from European Turkey are conspecific with *T. martinorum* from Bulgarian Thrace. *Talpa levantis* is therefore a species endemic to the Caucasus and the Pontic Mts. of south-western Asia.

Species delimitation in Levant moles. One of the central aims of our study was a translation of phylogenetic results into taxonomy. In the interpretation of Demirtaş et al. (2020) the Cyt *b* K2P divergence by 7.28% (8.0% maximum uncorrected distance in our results, 6.4% as a median) between their eastern and western sublineages (identical to Eastern and Western + Central lineages in this study) justify their ranking as distinct species, namely *Talpa levantis* s. str. and *T. transcaucasica*. Given that the K2P value of 7.28% is the lowest interspecific distance in the genus *Talpa*, Demirtaş et al. (2020) justified their taxonomic split by pointing on a “robust and geographically coherent” topology of their phylogenetic tree. Furthermore, they stressed that subterranean mammals are “morphologically constrained” which makes traditional delineation between species “intrinsically difficult”. Indeed, at least one newly recognized species of *Talpa*, i.e. *T. ognevi*, was elevated to the rank of species in its own right (Kryštufek & Motokawa 2018) entirely on the basis of genetic distances provided by Bannikova et al. (2015). On the other hand, two recent studies established new

species of *Talpa* (*T. aquitania* and *T. martinorum*) on the basis of both, genetic distances and unique craniodental traits (Nicolas et al. 2017, Kryštufek et al. 2018a) and the independent species status for *T. talyschensis* was proposed on morphological evidence (Zaytsev et al. 2014) before this was revealed by nucleotide sequences (Bannikova et al. 2015).

While ranking the three Cyt *b* lineages of Levant moles, we had the following in mind:

1. Genetic distances between the lineages of the Levant mole are below the lowest inter-specific pairwise distance in the genus *Talpa*.
2. Craniometric distances calculated in our study do not match the genetic distances. Genetically the most distinct were the Central and the Eastern lineages, while the greatest Mahalanobis squared D2 distance was retrieved between the Western and Central OTUs.
3. Univariate and multivariate analyses of morphometric variables displayed a pattern of a gradual longitudinal cline with no evidence of discontinuity on the contact zones of the three lineages. Such a smooth transition may not be due to a putative gene flow but can equally well indicate morphological response to the environment, which frequently changes gradually and was not tested in our study.
4. Our study retrieved a wide zone of overlap between the Western and Eastern lineages, which is most likely due to a secondary admixture of allopatrically evolved populations (Avice 2000). The Cyt *b* evidence on its own unfortunately does not allow a conclusion regarding gene flow, or lack of it, between the two lineages. Consulting more and nuclear markers would help future investigations on the topic.

We suggest a polytypic species concept as the appropriate taxonomic solution for the observed pattern of variation in the Levant mole. Subsequently we classify the three lineages as distinct subspecies. Subspecies are usually defined as allopatric groups of populations with independent histories, which are definable by geographically structured attributes, be they either, or both, morphological and molecular characteristics (Patton & Conroy 2017). As long as they are part of one and the same species, subspecies are by definition inter-fertile. Our hypothesis of three reproductively compatible, rather than reproductively isolated groups of populations of Levant moles can be falsified and is therefore testable. This hypothesis can be tested on the contacts of divergent phylogeographic lineages. We urge for further field sampling and molecular screening of moles in the zone of overlap between the Western and the Central lineages around the city of Zonguldak and to the west of it, and between Trabzon and Rize, where one can expect the Central and the Eastern lineages to meet.

Taxonomy of *Talpa levantis*

Talpa levantis Thomas, 1906

Diagnosis. Distinguishable from all other species of the genus *Talpa* by nuclear and mitochondrial DNA sequences (Bannikova et al. 2015, Demirtaş et al. 2020).

Description. *T. levantis* is a smaller mole (H&B=103–149 mm, CbL=28.6–33.5 mm) with eyelids sealed and the eyes covered by a transparent skin. External morphology shows no peculiarities. Skull is of average shape (Kryštufek et al. 2018a): relative width (as a percentage of CbL) of rostrum over canines is 11.8–14.9% and width of rostrum over molars is 24.7–31.0%. The maxillary tooth-row is comparatively short (MxT%=35.6–38.9%). However, the 1st upper molar has a parastyle, which shows heavy tooth-wear. The pelvis is of the caecoidal type, i.e., with the 4th sacral foramen opened posteriorly (Doğramacı 1989b). Diploid number of chromosomes is $2n = 34$ and the fundamental number of autosomal arms is $NFa = 64$. All subspecies were karyotyped and no variation was reported (Sokolov & Tembotov 1989,

Kefelioğlu & Gençoğlu 1996; Sevindik 2013, Selçuk & Kefelioğlu 2017).

Comparisons. *T. levantis* can be separated by morphological and karyological characteristics from other moles occupying Turkey (Kefelioğlu & Gençoğlu 1996, Kryštufek & Vohralík 2001, Kryštufek et al. 2018a). *T. ognevi* is larger (CbL= 33.6–35.9 mm) and has a higher diploid number ($2n = 38$; Selçuk & Kefelioğlu 2017). *T. davidiana* has a more robust skull with a comparatively wider rostrum; the breadth across canines accounts for 12.1–14.5% of the condylobasal length in *T. levantis* as opposed to 14.9–17.3% in *T. davidiana*. *T. levantis* is smaller than *T. europaea* from European Turkey (CbL=32.4–37.0 mm) and has eyelids grown together, while they are free in *T. europaea*. *T. levantis* has a parastyle on the 1st upper molar while *T. martinorum* lacks it. Overall comparison of cranial shape in Turkish species of *Talpa* is summarised in Selçuk et al. (2017).

Distribution. Range embraces the coast and mountains in northern Turkey along the Sea of Marmara and the

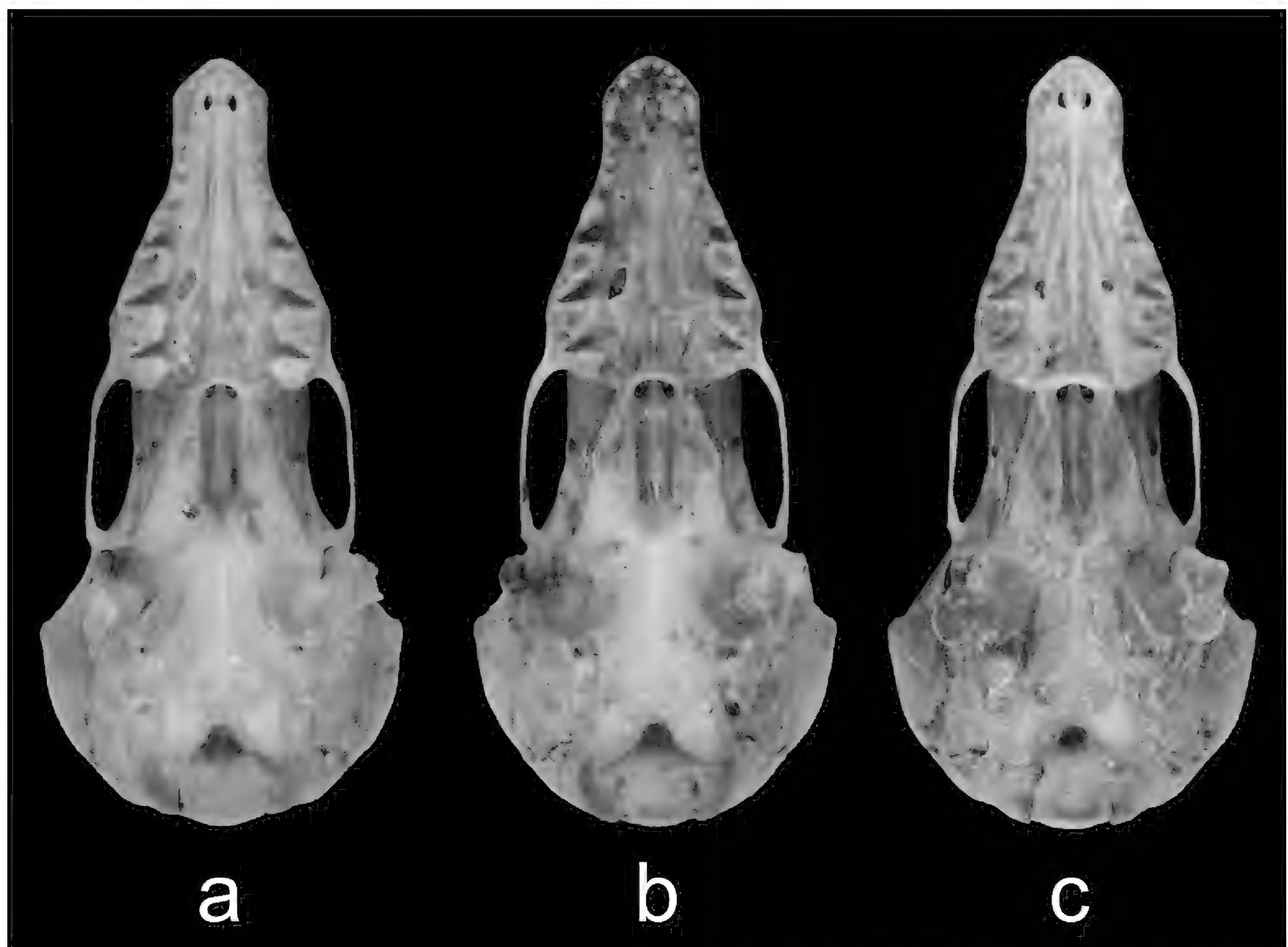


Fig. 6. Ventral cranium of subspecies of *Talpa levantis*. **a.** *T. l. dogramacii* ssp. nov. PMS 10650 (paratype; condylobasal length of skull = 30.2 mm). **b.** *T. l. levantis* PMS 10299 (31.3 mm). **c.** *T. l. transcaucasica* PMS 21658 (30.3 mm).

Black Sea (Fig. 1) and the Caucasus in Georgia, Armenia (as far south as Lake Sevan), and Russia (south of Kuban and Sulok rivers in Krasnodar, Adygea, Karachay-Cherkessia, Ingushetia, Chechnya, and Dagestan; Sokolov & Tembotov 1989). A population in the Lake Van area is obviously an isolate (Kryštufek & Motokawa 2018).

Miscellaneous. Reviewed by Kryštufek & Motokawa (2018); Sokolov & Tembotov (1989) provided a detailed review of the Caucasian populations. We subsequently list three subspecies (Fig. 6). The population from Lake Van was not assigned to any of them and requires a molecular screening.

***Talpa levantis levantis* Thomas, 1906**
(Fig. 5b)

Talpa caeca levantis Thomas, 1906:416. Type locality is “Scalita, S. of Trebizond”, now “Altındere, south of Trabzon, Turkey” (Kryštufek & Vohralik 2001:100). The type is a skin and skull in the Natural History Museum London (No. 6.3.6.5); type was seen.

Talpa levantis: Spitzenberger, 1973 (in Felten et al. 1973:229). First use of current name combination.

Diagnosis. Identical to the Central lineage of *Talpa levantis* as retrieved in the phylogenetic analysis of the mitochondrial Cyt *b* gene. In our dataset, the subspecies *levantis* has unique mutations in comparison with sequences of both ssp. *transcaucasica* and *T. l. dogramacii* new subspecies at 6 positions of our Cyt *b* alignment (see Appendix II): 150:C, 447:T, 852:G, 933:G, 990:T, 1020:T.

Description and comparison. Similar to the remaining subspecies and the differences are on average. The nominotypical subspecies differs significantly from ssp. *transcaucasica* in four linear variables (H&B, HfL, CbL, MxT) and both quotients (MxT%, RoM%) in males and in two linear variables (CbL, MxT) in females. The nominotypical subspecies attained higher means in all comparisons but had a relatively shorter maxillary tooth-row (MxT%) than ssp. *transcaucasica*. For comparison with *T. l. dogramacii* ssp. nov. see under that subspecies.

Distribution. The Black Sea coast and mountains from vicinity of Zonguldak to Trabzon. Endemic to Turkey.

***Talpa levantis transcaucasica* Dahl, 1945**
(Fig. 5c)

Talpa europaea transcaucasica Dahl, 1945: 48. The year of publication on the cover page is 1944; with 1945 we follow Pavlinov & Rossolimo 1998: 8). Type locality (p. 49): “Окресности села Воскресеновски (Кироваканский р-н Арм. ССР) ... Высота 1845 м

над уровнем моря [Surroundings of the village of Voskresenovka (Kirovakan district of the Armenian Soviet Socialist Republic) ... Altitude 1845 m above sea level]”. Since names of places changed since 1945, the type locality is now: Lermontovo (formerly Voskresenovka), Lori Province (formerly Kirovakan district), Armenia.

Talpa minima Deparma, 1959:31. Type locality is “Сев.-зап. Кавказ, верховья реки Белой, близ поселка Хамышки, 500 м ур. м.” – [“north-western Caucasus, the upper stream of River Beloy, near the settlement Khamyshki, 500 m a. s. l.”] (from Borissenko et al. 2001: 164), Adygea (Adyghe) Republic, Russia. In Deparma 1960: 97, the type locality is cited as: “Chamischki am Oberlauf des Flusses Belaja; NW-Kaukasus; 500 m ü. M. [Meter über Meereshöhe = metres above sea level]”

T[alpa] o[rientalis] transcaucasica: Vereschagin, 1959:388.

T[alpa] h[ercegoviensis] minima: Kuzyakin, 1965:50.

T[alpa] c[aece] minima: Gromov, Gureev, Novikov, Sokolov, Strelkov & Chapskiy, 1963:79.

T[alpa] l[evantis] minima: Sokolov & Tembotov, 1989:249.

T[alpa] l[evantis] transcaucasica: Sokolov & Tembotov, 1989:249. First use of current name combination.

T[alpa] transcaucasica: Demirtaş, Silsüpür, Searle, Bilton & Gündüz, 2020 (unpaginated early online release).

Diagnosis. Identical to the eastern sublineage of Demirtaş et al. (2020) and to the Eastern lineage of *Talpa levantis* as retrieved in this study through the phylogenetic analysis of the mitochondrial Cyt *b* gene. In our dataset, the subspecies *transcaucasica* has unique mutations in comparison with sequences of both the nominotypical subspecies and *T. l. dogramacii* new subspecies at the following positions of our Cyt *b* alignment (see Appendix 2): 42:T, 54:G, 162:G, 213:C, 219:T, 223:C, 225:A, 231:G, 246:T, 279:C, 396:A, 480:C, 603:T, 640:T, 651:C, 667:C, 675:G, 678:C, 858:G, 867:T, 913:T, 1008:T.

Description and comparison. Similar to the remaining subspecies and the differences are on average. For comparisons see under *T. l. dogramacii* ssp. nov. and the nominate subspecies.

Distribution. The north-eastern and eastern Black Sea coast, the Lesser Caucasus in north-eastern Turkey, Georgia, and Armenia, and the Greater Caucasus in Georgia and Russia.

Miscellaneous. Deparma published the taxonomic description and naming of *Talpa minima* in two papers, in Russian (Deparma 1959) and in German (Deparma 1960). This caused the inconsistency in reporting the year of publishing the name. While Russian authors con-

sistently quoted 1959 (Gureev 1979, Gromov et al. 1963, Kuzyakin 1965, Pavlinov & Rossolimo 1987, Sokolov & Tembotov 1989, Zaytsev et al. 2014), Western authors were aware only of the German version and cited 1960 (Hutterer 2005).

Sokolov & Tembotov (1989) recognized *minima* as subspecifically distinct from *transcaucasica*. The former is smaller (mean CbL is 28.66 mm in males and 28.25 mm in females) and occupies the western Caucasus; the latter is larger (mean CbL is 30.12 mm in males and 30.02 mm in females) and lives in the north-central Piedmont of the Greater Caucasus and the eastern Lesser Caucasus (Sokolov & Tembotov 1989).

***Talpa levantis dogramacii* ssp. nov.** Kefelioğlu, Kryštufek, Selçuk, Hutterer & Astrin (Figs. 6a, 7)

urn:lsid:zoobank.org:act:E3600CE0-7682-422B-830B-D0A6556FCD7B

Holotype and type locality. Skin, skull, pelvis and tissue sample in ethanol of an adult male (OMU 1352; Fig. 7); tissue also deposited in ZFMK (ZFMK-TIS-35886), collected by Ahmet Yesari Selçuk in March 2019 near Baraklı village, Mt. Uludağ, Bursa, Turkey (39.96056 N,

29.2633 E, 1100 m above sea level). DNA of this specimen has been deposited (ZFMK-DNA- FD02298704) at ZFMK, Bonn, and the cytochrome *b* sequence is available from GenBank (Accession number MT738557) and Appendix II.

Measurements of holotype. Body mass 58 g, head and body 120 mm, tail 28 mm, hind foot 18 mm, condylobasal length of skull 29.8 mm, maxillary tooth-row 11.6 mm, breadth of braincase 14.7 mm, breadth of rostrum over canines 4.0 mm, breadth of rostrum over molars 8.7 mm, greatest length of pelvis 22.1 mm, breadth of pelvis 11.9 mm.

Diagnosis. Identical to the Western lineage of *Talpa levantis* as retrieved in the phylogenetic analysis of the mitochondrial Cyt *b* gene. In our dataset, the new subspecies has unique mutations in comparison with sequences of both the nominotypical subspecies (corresponding to Central lineage) and *T. transcaucasica* (Eastern lineage) at five positions of our Cyt *b* alignment (see Appendix II): 522: T, positions 654, 731, 786, 1005: G. The new subspecies has a proportionally longer maxillary tooth-row, a proportionally broader rostrum over molars and the least bowed posterior margin of the braincase compared to the other two subspecies of *T. levantis*.

Paratypes. Three individuals collected on Mt. Uludağ and preserved as museum vouchers, tissue samples and with cytochrome *b* sequences deposited in the GenBank (see Table 1). OMU 1350, an unsexed individual; preserved as a skull; tissue ZFMK-TIS-35885; DNA sample: ZFMK-DNA- FD02298617; GenBank No. MT738556. OMU 1353: an unsexed individual; preserved as a skull; tissue ZMMU-TIS-35887; DNA sample: ZFMK-DNA- FD02298696; GenBank No. MT738558. All paratypes in OMU were collected in August 2018 by Ahmet Yesari Selçuk. PMS 10,650: a female collected on 30 June 1994 by B. Kryštufek, preserved as a skull, skin and postcranial skeleton; GenBank No. FN640571.

Measurements of paratypes. External measurements of a female PMS 10,650: body mass 55 g, head and body 118 mm, tail 28 mm, hind foot 17 mm. Skull measurements of OMU 1350, OMU 1353, and PMS 10,650: condylobasal length of skull 31.2, 29.8, 30.2 mm, maxillary tooth-row 12.1, 11.4, 11.8 mm, breadth of braincase 14.9, damaged, 14.4 mm, breadth of rostrum over canines 4.1, 4.1, 3.9 mm, breadth of rostrum over molars 8.9, 8.8, 8.9 mm.

Description and comparisons. *Talpa levantis dogramacii* ssp. nov. is of about the same external appearance and body proportions as the remaining subspecies of *T. levantis*. It differs significantly from the nominotypical subspecies by a shorter head and body (males), shorter

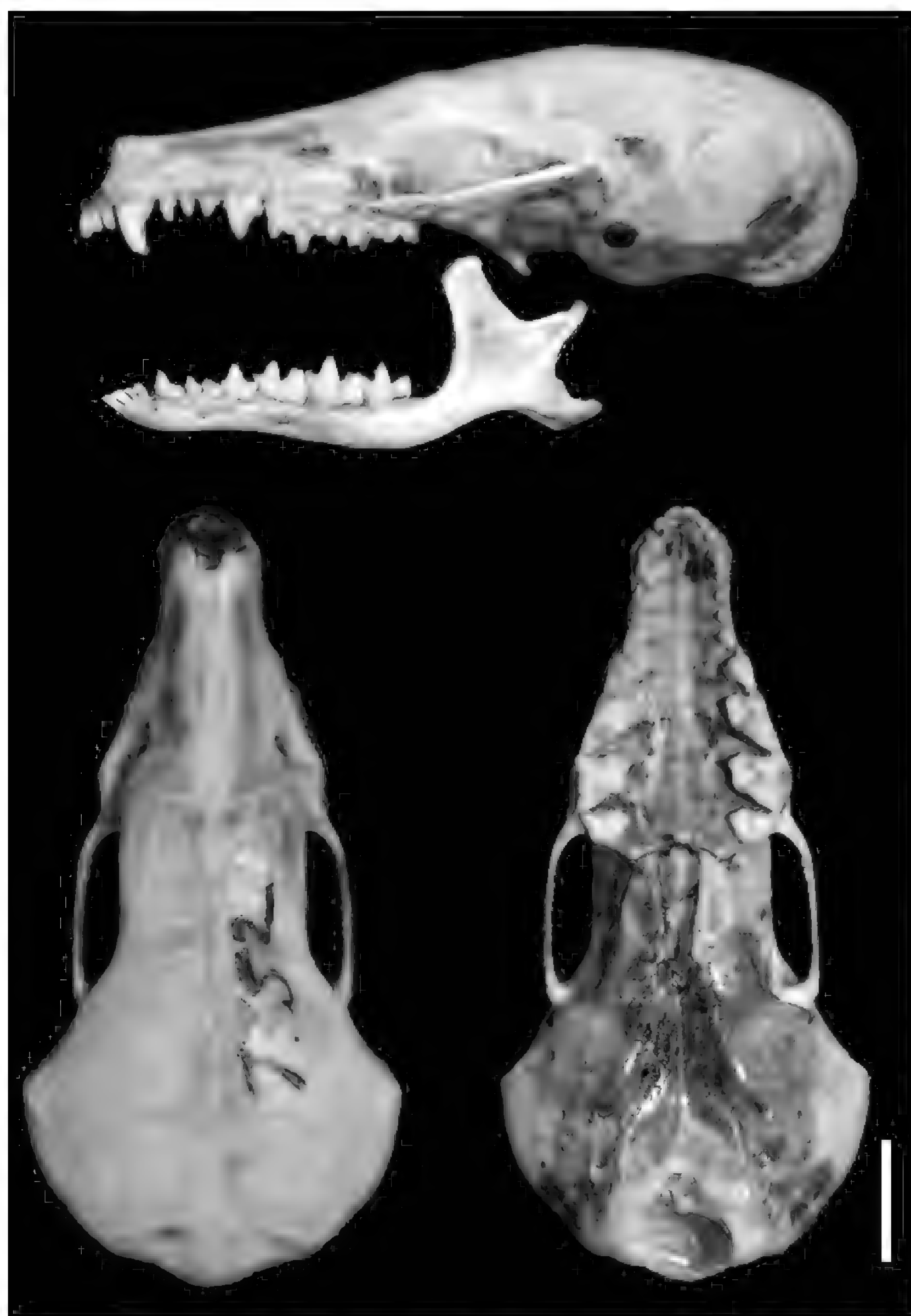


Fig. 7. Skull and mandible of the type specimen of *Talpa levantis dogramacii* ssp. nov. OMU 1352. Scale bar = 5 mm.

condylobasal length (females) and broader rostrum over molars (females). *Talpa l. dogramacii* ssp. nov. differs significantly from ssp. *transcaucasica* in having a longer maxillary tooth-row, both absolutely (in males) and relative to length of skull (in both sexes), a narrower breadth across molars, both absolutely and relative to length of skull (both in males; Table 2), and a less bowed posterior outline of the braincase (Fig. 3).

Distribution. The western-most part of the range of *T. levantis*, i.e., along the Anatolian coast of the Sea of Marmara and westward until Zonguldak.

Etymology. *Talpa levantis dogramacii* ssp. nov. is an eponym to Dr. Salih Dođramacı (1 July 1941, Elena, Bulgaria – 30 September 1993, Samsun; Fig. 8), a Professor of zoology at the Ondokuz Mayıs University, Samsun, and an outstanding Turkish mammalogist. Among others, Professor Dođramacı published works of crucial importance for the taxonomy of *Talpa* in Turkey (Dođramacı 1988, 1989a, b) and a revised list of Turkish mammals (Dođramacı 1989c). He published in Turkish and in journals with limited circulation outside of Turkey and is therefore not well known beyond his native country. Salih Dođramacı built an important research collection of Turkish small mammals with well prepared and meticulously labelled museum vouchers. The collection is deposited at the Ondokuz Mayıs University and also provided an invaluable source of information for the present study. *Microtus dogramacii* Kefelioğlu & Kryštufek, 1999, a species of social vole endemic to south-western Asia, is another eponym to the late Professor Dođramacı.

Miscellaneous. *Talpa levantis dogramacii* ssp. nov. was first recognized as distinct from *T. levantis* in a craniometric study (Kryštufek 2001) and was separated from *T. levantis* under the tentative name *Talpa caeca* (Kryštufek & Vohralík 2001).

Species of the genus *Talpa* in Turkey

Demirtaş et al. (2020) stressed that Turkey is “home to six distinct species [of moles], more than any other comparable geographical region” which “[emphasises] the importance of this region as a global centre of mole diversification.” Measuring, quantifying and comparing biodiversity can be tricky when dealing with a complex geopolitical entity like Turkey. First, the country spreads across two continents, which since the last glacial maximum were separated by the sea, but in the past were intermittently connected by a land bridge. As discussed above, the land bridge at the Turkish straits both facilitated and filtered the transcontinental faunal migrations. As poor dispersers (Kryštufek & Motokawa 2018) moles were obviously filtered by this land corridor. As we have seen, our study falsified the hypothesis of Demirtaş et al.



Fig. 8. Dr. Salih Dođramacı and his wife (Foto Yener, Ankara).

(2020) regarding the transcontinental range of *Talpa levantis*. The two sides of the Turkish straits have no mole species in common and their species evolved in different centres of diversification, the south-eastern European centre and in south-west Asia with further two similar centres.

Moles with restricted distributions are usually endemic to the Quaternary refugia and each of the main south-eastern-European peninsulas has at least two small-range endemics of the genus *Talpa* (cf. Kryštufek & Motokawa 2018). The number of mole endemics is remarkably similar between centres of endemism being either two or three endemics per centre (Table 3). Turkey does not contain all endemics from any of the three centres it encompasses, but on the other hand, comprises three out of total five such centres, as we know them in the western Palearctic (Table 3). The number of centres encompassed by Turkey is the reason for the sum of partial regional species numbers, which is high enough to rank the country higher than any other in the species richness of the genus *Talpa*. This conclusion does not downgrade the high biodiversity richness of Turkey, but makes it explicable.

Subsequently, we briefly review mole species, other than *T. levantis*, occupying Turkey. The genus has been reviewed by Dođramacı (1989a), Kefelioğlu & Gençoğlu (1996), and Kryštufek & Vohralík (2001). For karyotypes see Sevindik (2013; for *T. europaea*), Kefelioğlu & Gençoğlu (1996; *T. ognevi*), and Sözen et al. (2012; *T. davidiana*).

Table 3. Presence of moles in five centers of endemism. Presences in Turkey are shown by dots. *Talpa europaea* is a widespread species while the remaining moles are endemic to two centres (*T. caeca*) or a single centre (the rest). Centres of endemism: Ip – Iberian Peninsula; It – Italian Peninsula; Ba – Balkan Peninsula; PC – Pontic Mts. and the Caucasus; AH – Anatolian-Iranian High Plateau and the Hyrcanian coast. Based on Kryštufek & Motokawa (2018).

Species	Centre of endemism				
	Ib	It	Ba	PC	AH
<i>T. europaea</i>		○	●		
<i>T. occidentalis</i>	○				
<i>T. aquitania</i>	○				
<i>T. romana</i>		○			
<i>T. caeca</i>		○	○		
<i>T. stankovici</i>			○		
<i>T. martinorum</i>			●		
<i>T. levantis</i>				●	
<i>T. ognevi</i>				●	
<i>T. caucasica</i>				○	
<i>T. davidiana</i>					●
<i>T. talyschensis</i>					○
Species total	2	3	4	3	2

***Talpa europaea* Linnaeus, 1758**

Talpa europaea Linnaeus, 1758:52. Type locality (originally Europe) subsequently restricted to Sweden, Kristianstad, Engelholm.

Reported for Turkey by Osborn (1964). Occupies European Turkey; range mapped by Doğramacı (1989a).

***Talpa martinorum* Kryštufek, Nedyalkov, Astrin & Hutterer, 2018**

Talpa martinorum Kryštufek, Nedyalkov, Astrin & Hutterer, 2018 (Kryštufek et al. 2018a:45). Type locality: near Zvezdets, Mt. Strandzha, Bulgaria.

Reported for Turkey as *Talpa caeca* Savi, 1822 (Osborn 1964, Doğramacı 1988, 1989b), and afterwards as *T. levantis* (Vohralík 1991, Kryštufek & Vohralík 2001). Presence in eastern Turkish Thrace postulated by Kryštufek et al. (2018a) and for the first time confirmed in this study.

***Talpa ognevi* Stroganov, 1944**

Talpa romana ognevi Stroganov, 1944:131. Type locality: “Бакуриани, Грузия [Bakuriani, Georgia]”.

Reported for Turkey as *Talpa caucasica* Satunin, 1908 (Doğramacı 1989b). The name *ognevi* was elevated to species in Kryštufek & Motokawa (2018), following the evidence provided by Bannikova et al. (2015). Range is in Georgia and NE Turkey (Hopa region).

***Talpa davidiana* (A. Milne Edwards, 1884)**

Scaptochirus davidianus A. Milne Edwards, 1884:1143. Type locality: “environs d’Akbes, sur les confins de la Syrie et de l’Asie Mineure” (p. 1142), now Meydanekbez, southwest of Gaziantep, Turkey (Kryštufek et al. 2001:140)

Earlier reported for Turkey as *Talpa streeti* Lay, 1965; the name is a junior synonym of *Scaptochirus davidianus*, which is a member of the genus *Talpa* (Kryštufek et al. 2001). Occupies south-eastern Turkey and Lake Van area (Kryštufek et al. 2001, Sözen et al. 2012).

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APPENDICES

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APPENDIX I.

The list of museum vouchers used in this study.

APPENDIX II.

Sequencing of the new Turkish samples.

APPENDIX III.

Table S1. Results of regression analysis of morphometric variables and two quotients against the latitude for *Talpa levantis* in Northern Anatolia. Shown are only variables showing significant correlation coefficient (at $p < 0.05$). Acronyms for traits are explained in text.

Table S2. Summary statistics for the principal components analysis on five cranial measurements transformed to logarithms. One-way Anova was performed with OTU as the categorical value. Acronyms for skull measurements are explained in text.

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Hitherto unknown and poorly known sexual morphs of three Asiatic species of the aphid genus *Uroleucon* (Hemiptera: Aphididae)

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Abstract. In this paper, we describe hitherto unknown and redescribe poorly known sexual morphs (oviparous females and males) of three Asiatic species of the Macrosiphini genus *Uroleucon* Mordvilko, 1914. The oviparous female of *Uroleucon* (*Uromelan*) *amamianum* (Takahashi, 1930) is described in detail as well as the oviparous female and alate male of *U. (Uroleucon) fuchuense* (Shinji, 1942). The hitherto unknown oviparous female of *U. (U.) formosanum* (Takahashi, 1921) is described and the poorly known alate male is redescribed. Notes about distribution and host plants of these species are also given.

Key words. Aphids, description, *U. amamianum*, *U. formosanum*, *U. fuchuense*.

INTRODUCTION

Uroleucon Mordvilko, 1914 (Hemiptera: Aphididae: Macrosiphini), which comprises about 241 species within six subgenera, is regarded as one of the most speciose genus within the macrosiphines (Favret 2020). Members of *Uroleucon* are characterised by particularly often divergent antennal tubercles, apterous viviparous females with secondary rhinaria on the antennal segment III, quite a long terminal process and long and cylindrical siphunculi with a developed area of subapical reticulation. The cauda is often long and finger shaped, and the first segments of the tarsi usually have five, and in several species three or four setae. The abdomen of most *Uroleucon* species bears rounded or oval scleroites and quite long setae (Heie 1995; Blackman 2010; Blackman & Eastop 2020). More than 170 species live on herbaceous plants that belong to Asteraceae and Campanulaceae (Blackman 2010; Blackman & Eastop 2020). *Uroleucon* representatives have so far been described and recorded from almost all continents and zoogeographical regions including the East Palaearctic.

Apterous and alate viviparous females are the most well-known morphs of almost every species that has been described including *Uroleucon* in the East Palaearctic (e.g., Takahashi 1921; 1923; 1924; Miyazaki 1971; Pashchenko & Lobkova 1990; Pashchenko 2001). On

the other hand, in many cases, the sexual morphs (oviparous females and males) of many aphids are still poorly known or unknown, and have very rarely been collected and described. Despite this rarity, the importance of the sexual generation has been proven in the expansion of our knowledge of the general biology of poorly known species, but also by solving taxonomical problems or improving our understanding of the evolution of aphids (Ilharco 1965; Wieczorek et al. 2013; Depa et al. 2015; Pérez Hidalgo et al. 2016; Kanturski et al. 2017; Nowińska et al. 2017; Stekolshchikov & Buga 2017; Kanturski et al. 2018; Mier Durante et al. 2020).

In the Republic of Korea, a total of 20 species of *Uroleucon* have been recorded to date (Lee et al. 2002a; Lee et al. 2002b; Choi et al. 2012; Choi 2019). However, there has been little research on their sexual morphs. During an examination of the aphid collection in the Biology Centre of the Czech Academy of Sciences, Institute of Entomology, České Budějovice (Czech Republic), specimens of unknown and poorly known sexual morphs of three native East Palaearctic species of *Uroleucon* collected by the late J. Holman were discovered. We describe the oviparous female of *U. (Uromelan) amamianum* (Takahashi, 1930), the oviparous female and alate male of *U. (Uroleucon) fuchuense* (Shinji, 1941) and *U. (Uroleucon) formosanum* (Takahashi, 1921) and redescribe the poorly known alate male of the latter.

MATERIAL AND METHODS

The specimens were examined using a Leica DM 3000 LED light microscope and photographed using a Leica MC 190 HD camera using a differential interference contrast. The measurements were done according to Ilharco and van Harten (1987). The current host plant names are given according to The Plant List (2013).

The following abbreviations are used: ABD: abdominal tergite; ANT: antennae or their lengths; ANT I–VI: antennal segments I, II, III, IV, V, VI or their lengths (ratios between antennal segments are simply given as e.g. ‘VI: III’); BASE: basal part of last antennal segment or its length; BD III: basal articular diameter of ANT III; BL: body length (from the anterior border of the head to the end of cauda); III FEMORA: hind femora or their length; HW: greatest head width across the compound eyes; HT I: first segment of the hind tarsus; HT II: second segment of the hind tarsus or its length; LS ANT III: length of the longest setae of ANT III; PT: processus terminalis of the last antennal segment or its length; SIPH: siphunculus or its length; III TIBIAE: hind tibiae or their

length; URS: ultimate segments of the rostrum (IV + V) or their lengths. In the case of a series of single slides with a single specimen with the same collection data for the examined material sections, all of them present the same data as the full previous slide in order to avoid repetition. The terminology of the male genitalia follows Wieczorek et al. (2011). The photos of apterous viviparous females of *U. formosanum* in Figure 6a and 6b are used with permission of JADAM Organic Farming, <http://en.jadam.kr/news/articleView.html?idxno=10121> (Daejeon, Republic of Korea)

The material examined is deposited in IECA — the Biology Centre of the Czech Academy of Sciences, Institute of Entomology, České Budějovice (Czech Republic);

RESULTS

Uroleucon (Uromelan) amamianum (Takahashi, 1930)
Figs 1–2

Macrosiphum amamianum Takahashi, 1930: 318



Fig. 1. Oviparous female of *Uroleucon amamianum*.

Dactynotus amamianus Takahashi, 1962: 76

Uroleucon (*Uromelan*) *amamianum* Eastop & Hille Ris Lambers, 1976: 255

The apterous viviparous females of this species are bright shiny red to reddish brown with black antennae, siphunculi, cauda and distal halves of the femora (Takahashi 1930; Blackman & Eastop 2020). According to Miyazaki (1971), *Uroleucon amamianum* is similar to *U. lactucico-*

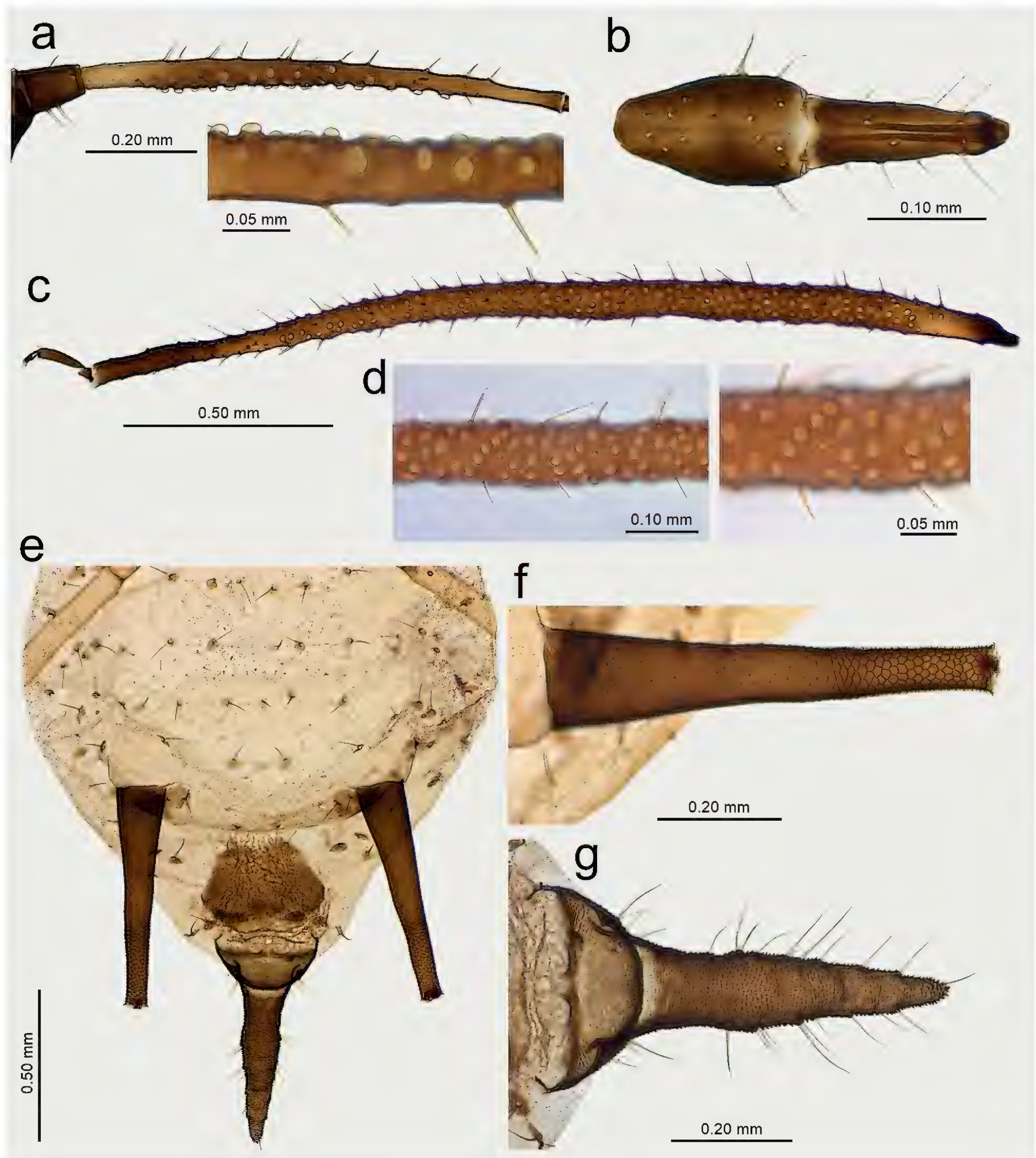


Fig. 2. Oviparous female of *Uroleucon amamianum*, morphological details. **a.** ANT III secondary rhinaria. **b.** Third and ultimate rostral segments. **c.** Hind tibia with scent plaques distribution. **d.** Scent plaques, detailed view. **e.** Abdomen. **f.** Siphunculus. **g.** Cauda.

la (Strand, 1928) due to the rather small and flat primary rhinarium on ANT V but differs in the ratio of the SIPH/cauda, which is less than 1.33 in the apterous viviparous females. This is quite a poorly known species, which as yet is only known from Japan and Korea. Miyazaki (1971) collected many apterous and alate viviparous females mostly from *Solidago virga-aurea* and *Aster* sp. in Japan. In The Republic of Korea, the species was recorded for the first time by Lee et al. (2002a), and was later reviewed with other species of the genus *Uromelan* by Choi et al. (2012), which found it on *Aster pinnatifidus*, *A. maackii*, *Patrinia scabionsaeifolia*, *Picris hieracioides*, *Solidago virga-aurea* var. *asiatica* and *S. virga-aurea* var. *gigantus*. Choi (2019) redescribed the apterous and alate viviparous female but no sexual morphs were included.

Oviparous female – description (n = 10)

Figs 1–2

Colour in life. Unknown. Pigmentation on slide: head brown; ANT I–II dark brown; ANT III brown with paler bases and sometimes with paler distal end; ANT IV–VI brown; pronotum and mesonotum usually with sclerotisation, brown; femora yellow with brown to dark brown distal halves; fore and middle tibiae with yellow middle section and dark brown bases and apices; hind tibiae brown to dark brown, sometimes with slightly paler sections near the proximal and distal ends but the very ends are always dark brown; tarsi dark brown; abdomen yellow with brown sclerites and scleroites; SIPH uniformly dark brown, cauda dark brown (Fig. 1).

BL 3.10–3.42 mm. HW 0.57–0.59 mm, $0.15\text{--}0.16 \times \text{ANT}$. Head with long, rigid setae with mostly pointed apices, 0.075–0.110 mm long. ANT tubercles each with 2–3 setae on internal angles. ANT 3.44–3.66 mm, $1.03\text{--}1.17 \times \text{BL}$. ANT III 0.81–0.87 mm with 27–38 protuberant, rounded or oval, different-sized secondary rhinaria with sclerotised rims, 0.01–0.02 mm in diameter (Fig. 2a), ANT IV 0.63–0.67 mm, ANT V 0.56–0.60 mm. ANT VI 1.14–1.27 mm, BASE 0.19–0.21 mm, PT 0.95–1.08 mm, $4.57\text{--}5.68 \times \text{BASE}$. Other antennal ratios: VI:III 1.37–1.49, V:III 0.67–0.69, IV:III 0.75–0.77, PT:III 1.12–1.27, PT:IV 1.50–1.63, PT:V 1.65–1.89. ANT chaetotaxy: ANT have thick, rigid setae with slightly blunt or narrow capitate apices. ANT III setae 0.03–0.05 mm long, LS ANT III $1.12\text{--}1.25 \times \text{BD III}$. ANT I with 10–11, ANT II with 4, ANT III with 20–26, ANT IV with 12–14, ANT V with 8–12 setae. ANT VI with 2–3 basal, 3–4 apical and 4–6 setae along the PT. Rostrum reaching hind coxae. URS 0.16–0.17 mm, $0.18\text{--}0.20 \times \text{ANT III}$, $0.12\text{--}0.14 \times \text{ANT VI}$, $0.14\text{--}0.17 \times \text{PT}$, $0.80\text{--}0.89 \times \text{BASE}$ and $1.30\text{--}1.36 \times \text{HT II}$ with 8–9 fine, pointed accessory setae (Fig. 2b). Mesosternal furca fused, wide, without stem. III FEMORA 1.22–1.25 mm with medium-length to long, stiff, rigid setae with pointed or slightly blunt apices, 0.020–0.05 mm long. III TIB-

IAE 2.17–2.25 mm, swollen with large number (c. 300–330) of rounded to oval or some 8-shaped scent plaques (pseudosensoria) on entire area and length (besides the very ends) (Fig. 2c–d). Setae on III TIBIAE rigid with mostly pointed or slightly blunt apices, 0.020–0.085 mm long. HT I with 3:3:3 setae, HT II 0.12–0.13 mm, $0.14\text{--}0.15 \times \text{ANT III}$, $0.09\text{--}0.11 \times \text{ANT VI}$, $0.11\text{--}0.13 \times \text{PT}$ and $0.61\text{--}0.65 \times \text{BASE}$. Abdomen membranous, with well-visible, rounded and irregular scleroites in spinal, dorsal and marginal areas (Fig. 2e), without marginal tubercles with medium-length to long, thick, rigid setae with pointed or slightly blunt apices, 0.055–0.110 mm long on ABD TERG I–V and 0.070–0.120 mm long on ABD TERG VI–VIII. ABD VIII with 8–9 setae. SIPH 0.67–0.70 mm, tubular, tapering, straight with distinct zone of subapical reticulation, well-developed postsiphuncular sclerites and small flange (Fig. 2f). Reticulated zone $0.31\text{--}0.37 \times \text{SIPH}$. SIPH $1.22\text{--}1.40 \times \text{cauda}$, $0.20\text{--}0.21 \times \text{BL}$ and $0.79\text{--}0.82 \times \text{ANT III}$. Genital plate with 2–3 anterior, 6–12 median and 28–29 posterior setae. Cauda 0.49–0.57 mm long and 0.19–0.22 mm wide, tapering, slightly constricted near base, $2.27\text{--}3.00 \times$ its width at base and $0.15\text{--}0.16 \times \text{BL}$ with 22–26 fine, pointed setae of two lengths (Fig. 2g).

Material examined. REPUBLIC OF KOREA, Gyeonggi-do, Pocheon-si, Gwangneung Royal Tomb Arboretum, Dendrological Park, 19 October 2000, *Solidago virgaurea*, J. Holman leg., 1 oviparous female, 1 apterous viviparous female, 00Ho75 (ovipara 9–10) (IECA), 2 oviparous females, 00Ho75 (ovipara 19–20), 2 oviparous females, 00Ho75 (ovipara 21–22), 1 oviparous female, 1 apterous viviparous female 00Ho75 (ovipara 23–24), 2 oviparous females, 00Ho75 (ovipara 25–26), 2 oviparous females, 00Ho75 (ovipara 27–28).

Uroleucon (Uroleucon) formosanum (Takahashi, 1921) Figs 3–6

Macrosiphum formosanum Takahashi, 1921: 6

Dactynotus (Dactynotus) formosanus Takahashi, 1962: 74

Uroleucon formosana Ghosh et al. 1970: 390

This species is one of the most commonly recorded *Uroleucon* in Eastern Asia, feeds mostly on species of *Lactuca*, *Ixeris*, *Picris*, *Sonchus* and others (Higuchi & Miyazaki 1969; Holman 2009) and can be easily recognised by its very long ANT III (in comparison to ANT IV and V) and large and extremely protuberant secondary rhinaria. Apterous viviparous females are shining red-brown with a broad black patch on the proximal part of the abdomen, black siphunculi and a pale yellow cauda (Fig. 3a–b). Alate viviparous females are similar in colour, with dark dorsal side of thorax and darker ventral side of abdomen (Fig. 3c). The species was described from Taiwan based

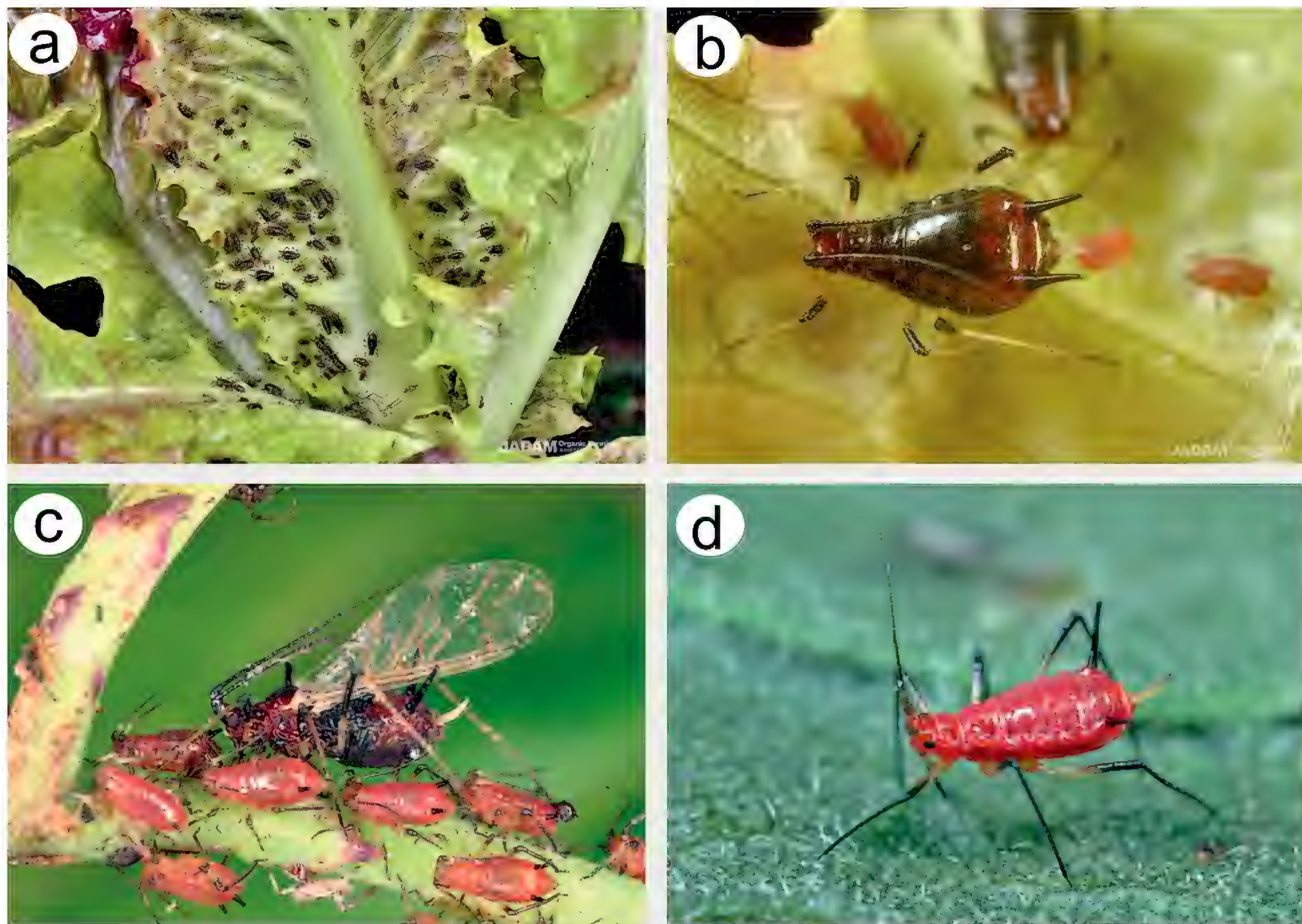


Fig. 3. *Uroleucon formosanum* viviparous generation on *Lactuca* and *U. fuchuense* in Korea. **a.** Colony of apterous viviparous females and larvae of *U. formosanum*. **b.** Apterous viviparous female of *U. formosanum* colour. **c.** Alate viviparous female of *U. formosanum* colour **d.** Apterous viviparous female of *U. fuchuense* colour.

on the viviparous generation (Takahashi 1921). In the same paper, Takahashi gave information that in November sexual morphs were observed near Tokyo in Japan, but not in Taiwan. Later, Takahashi provided information that the alate males and oviparous females occur in Japan from the last part of October until the end of November, whereas near Taihoku, the viviparous generations were observed throughout the year (Takahashi 1923). Shinji (1941) redescribed the viviparous generation and gave only a brief description of the alate male but as his monograph is in Japanese, the information was not available for a broad group of researchers. As for the occurrence, besides Taiwan (Takahashi 1921, 1923, 1924), the Korean Peninsula (Okamoto & Takahashi 1927; Lee et al. 2002b; Choi 2019; Choi et al. 2019) and Japan (Takahashi 1921; Shinji 1941; Miyazaki 1971; Sorin 1992; Sorin & Arakawa 2005; Adachi & Yoshitomi 2012, 2013; Yoshitomi 2014a, b, 2015), *U. formosanum* is known from China (Lou 1935; Tao 1963, 1968), India (Ghosh et al. 1970), Russian Far East (Pashchenko 1988, 2000) and Vietnam (Szelegiewicz 1968) in Asia. The species has been also recorded from Mariana Islands (Microne-

sia) which belong to the USA (Miller et al. 2003). Pike et al. (2005) provided a detailed redescription of the apterous and alate viviparous female during the comparison with *U. sonchellum* but the sexual generation was still not included.

Oviparous female – description (n = 9)

Figs 4–5

Colour in life. very similar to the apterous viviparous female (Shinji 1941). Pigmentation on slide: head and thorax dark brown; ANT uniformly brown to dark brown with sometimes slightly paler distal parts of ANT IV and ANT V; femora yellow with dark brown distal halves; fore and middle tibiae yellow middle sections and dark brown proximal and distal ends; hind tibiae brown with slightly paler distal half and dark brown proximal and distal ends; tarsi dark brown; abdomen yellow with brown sclerites and scleroites; SIPH uniformly dark brown, cauda yellow or pale (Fig. 4a).

BL 2.77–3.57 mm. HW 0.50–0.55 mm, $0.14\text{--}0.17 \times \text{ANT}$. Head with medium-length, fine, rigid setae

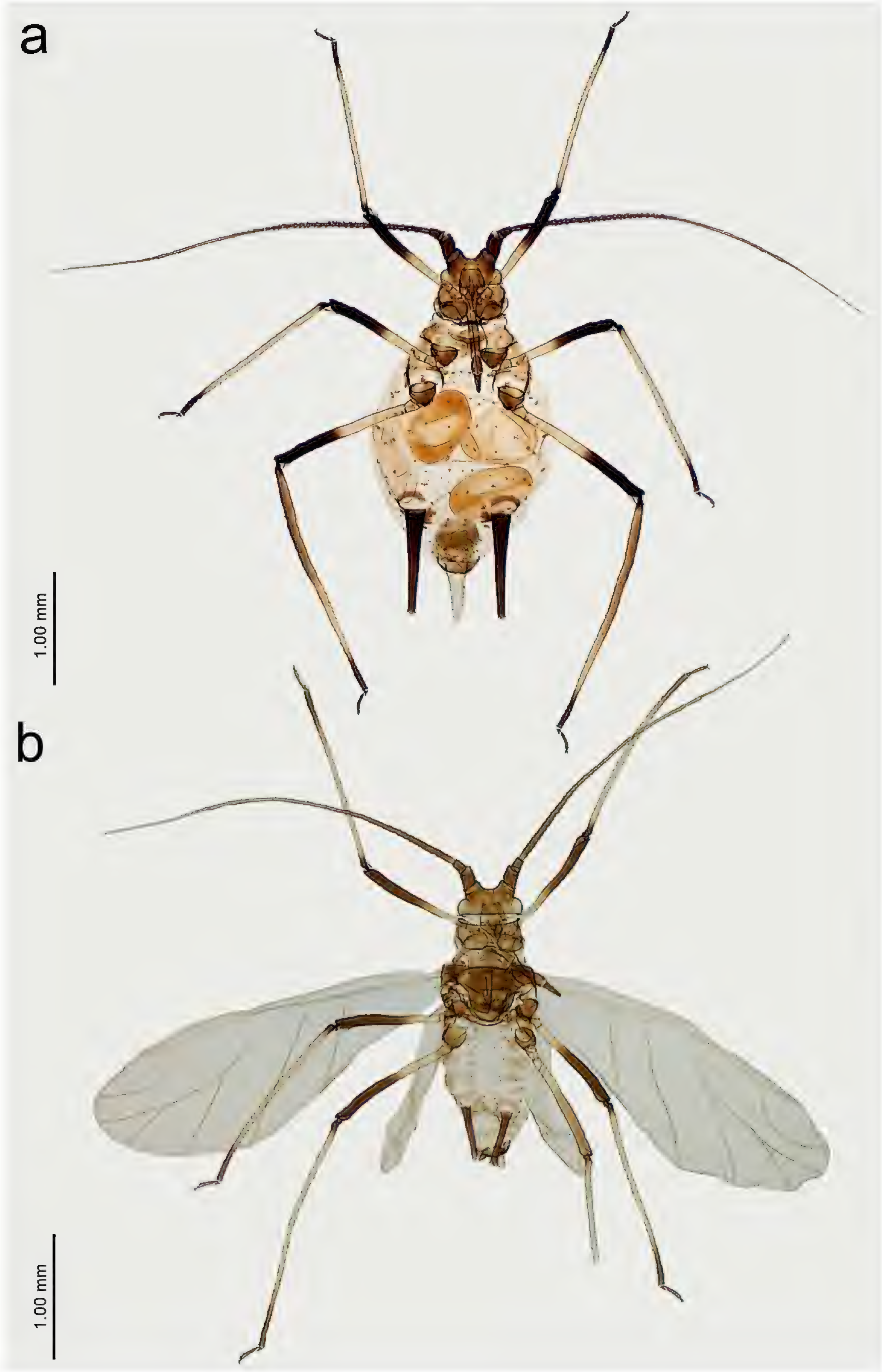


Fig. 4. Sexual morphs of *Uroleucon formosanum*. **a.** Oviparous female. **b.** Alate male.

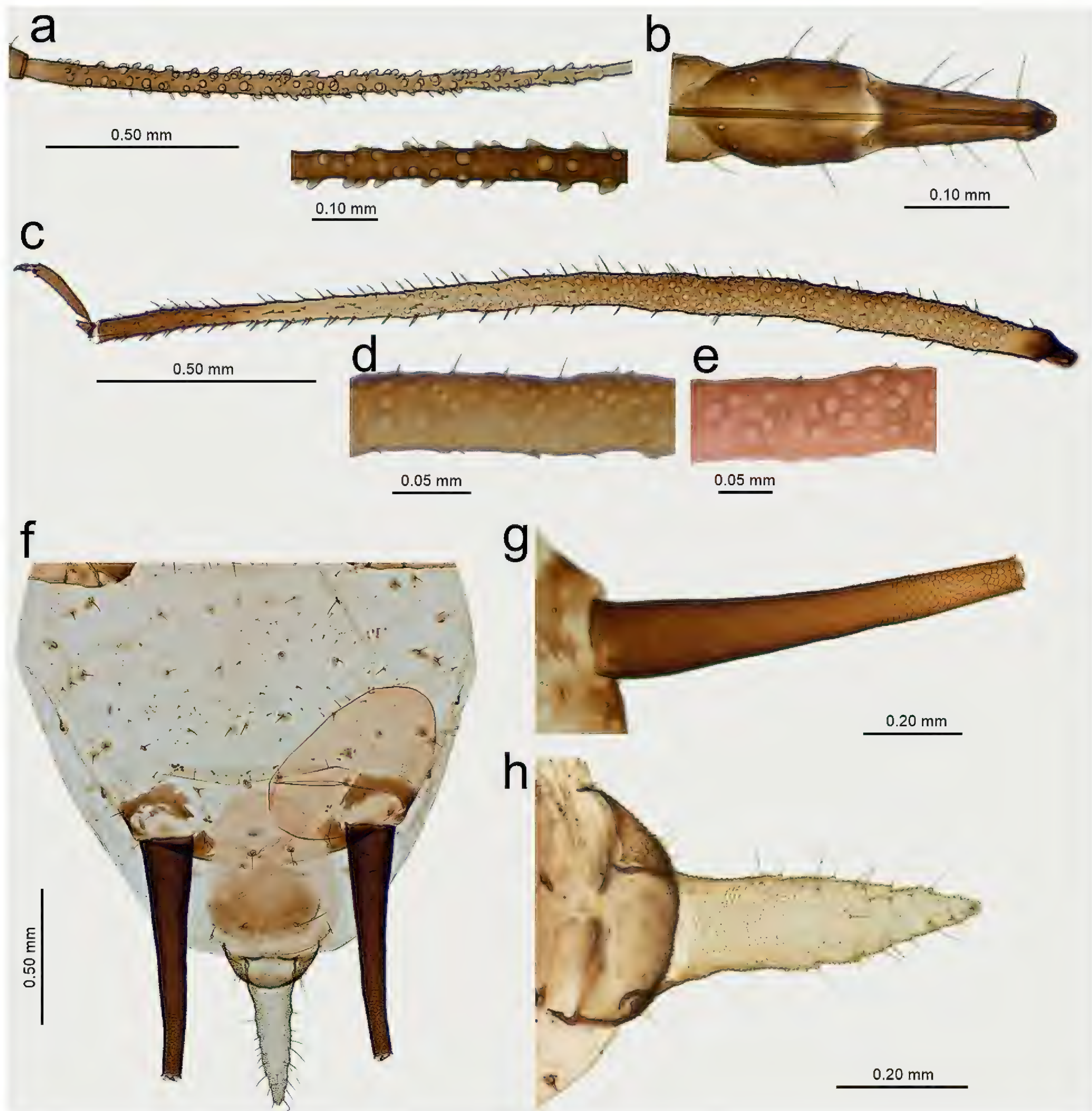


Fig. 5. Oviparous female of *Uroleucon formosanum*, morphological details. **a.** ANT III secondary rhinaria. **b.** Third and ultimate rostral segments. **c.** Hind tibia with scent plaques distribution. **d–e.** Scent plaques, detailed view. **f.** Abdomen. **g.** Siphunculus. **h.** Cauda.

with mostly pointed apices, 0.035–0.070 mm long. ANT tubercles each with 2–3 setae on internal angles. ANT 2.93–3.73 mm, $1.04\text{--}1.09 \times \text{BL}$. ANT III very long, 1.15–1.57 mm, with 78–110 mostly rounded and oval, different-sized and extremely protuberant secondary rhinaria, without sclerotised rims (Fig. 5a), ANT IV 0.31–0.41 mm, ANT V 0.30–0.41 mm. ANT VI 0.89–1.07 mm, BASE 0.12–0.16 mm, PT 0.77–0.92 mm, $5.56\text{--}6.41 \times \text{BASE}$. Other antennal ratios: VI:III 0.66–0.77, V:III 0.24–0.27,

IV:III 0.25–0.26, PT:III 0.56–0.66, PT:IV 2.22–2.56, PT:V 2.24–2.56. ANT chaetotaxy: ANT bearing thick, rigid setae with mostly pointed or slightly blunt apices. ANT III setae 0.020–0.035 mm long, LS ANT III $0.62\text{--}0.87 \times \text{BD III}$. ANT I with 6–7, ANT II with 4, ANT III with 18–26, ANT IV with 5–6, ANT V with 5–7 setae. ANT VI with 3–4 basal, 4 apical and 4–5 setae along the PT. Rostrum reaching hind coxae. URS 0.17 mm, $0.10\text{--}0.14 \times \text{ANT III}$, $0.15\text{--}0.19 \times \text{ANT VI}$, $0.18\text{--}0.22 \times \text{PT}$,

1.06–1.41 \times BASE and 0.94–1.03 \times HT II, with 8–9 short, fine, pointed accessory setae (Fig. 5b). Mesosternal furca fused, wide and robust, without or with poorly-developed and very stem. III FEMORA 1.05–1.30 mm, bearing medium-length to long, thick, rigid setae with mostly pointed or slightly blunt apices, 0.020–0.045 mm long. III TIBIAE 1.87–2.30 mm, swollen in the proximal part with large number (c. 313–343) of mostly rounded or slightly irregular scent plaques (pseudosensoria) on the entire area and length (besides the very ends) (Fig. 5c–e). III TIBIAE bearing rigid setae with mostly slightly pointed apices, 0.020–0.055 mm long. HT I with 5:5:5 ventral setae, HT II 0.16–0.18 mm, 0.11–0.14 \times ANT III, 0.16–0.18 \times ANT VI, 0.19–0.21 \times PT and 1.12–1.37 \times BASE. Abdomen membranous, with small but well-visible, rounded or irregular sclerites in spinal, dorsal and marginal area, without marginal tubercles, with medium-length to long, rigid setae with pointed apices, 0.035–0.075 mm long on ABD TERG I–V and 0.040–0.085 mm long on ABD TERG VI–VIII. SIPH with well-developed antesiphuncular and postsiphuncular sclerites (Fig. 5f). SIPH 0.67–0.90 mm, tubular, tapering, rather straight, with distinct zone of subapical reticulation and flange (Fig. 5g). The reticulated zone 0.24–0.29 \times SIPH. SIPH 1.26–1.69 \times cauda, 0.24–0.26 \times BL, and 0.54–0.60 \times ANT III. Genital plate with two anterior setae that are longer than the others, 8–14 median and 18–21 posterior setae. Cauda finger-shaped, 0.53–0.55 mm, long and 0.17–0.22 mm wide, 2.40–3.11 \times its width at base and 0.15–0.19 \times BL, with 26–28 fine setae of two lengths (Fig. 5h).

Alate male – redescription (n = 4)

Figs 4, 6

Colour in life. Unknown. Pigmentation on slide: head and thorax brown; ANT brown except basal part of ANT III and ANT VI PT which are paler; coxae brown; femora brown with yellow proximal parts or halves; tibiae with yellow middle section and brown apices; tarsi brown; SIPH brown; cauda pale (Fig. 4b).

BL 2.07–2.55 mm. HW 0.44–0.48 mm, 0.16–0.17 \times ANT. Head with fine, rigid setae with pointed apices, 0.025–0.040 mm long. ANT tubercles each with 3–4 setae on internal angles. ANT 2.58–3.00 mm, 1.17–1.30 \times BL. ANT III long, 0.91–1.05 mm, with 56–80 mostly rounded, different-sized, secondary rhinaria with sclerotised rims located on the whole length and surface (Fig. 6a–b), ANT IV 0.28–0.37 mm, with only 3–5 secondary rhinaria (Fig. 6c). ANT V, 0.29–0.39 mm, with 5–13 secondary rhinaria (Fig. 6d). Primary rhinaria rims on ANT V and VI with delicate projections (Fig. 6e, f). ANT VI 0.88–1.01 mm, BASE 0.12–0.15 mm, PT 0.76–0.86 mm, 5.64–6.33 \times BASE. Other antennal ratios: VI:III 0.88–1.01, V:III 0.31–0.37, IV:III 0.30–0.37, PT:III 0.75–0.86, PT:IV 2.19–2.71, PT:V 2.25–2.62. ANT has short, thick, rigid setae with slightly pointed

or blunt apices. ANT III setae 0.015–0.030 mm long, LS ANT III 0.71–0.83 \times BD III. ANT I with 46–7, ANT II with 4, ANT III with 22–26, ANT IV with 7, ANT V with 6–8 setae. ANT VI with 3–4 basal, 4 apical and 4–5 setae along the PT. Rostrum reaching metasternum. URS 0.14–0.16 mm, 0.14–0.16 \times ANT III, 0.15–0.16 \times ANT VI, 0.18–0.19 \times PT, 1.06–1.20 \times BASE and 0.93–1.06 \times HT II, with 7–8 fine, pointed accessory setae (Fig. 6g). III FEMORA 0.83–0.92 mm, with short to medium-length, thick, rigid setae with pointed or blunt apices, 0.012–0.035 mm long. III TIBIAE 1.45–1.82 mm, have thick, rigid setae with mostly pointed or blunt apices, 0.004–0.045 mm long. HT I with 5:5:5 ventral setae, HT II 0.14–0.16 mm, 0.15 \times ANT III, 0.14–0.17 \times ANT VI, 0.10–0.20 \times PT and 1.00–1.16 \times BASE. Abdomen membranous, with rounded or oval sclerites, without marginal tubercles with medium-length, fine setae with pointed apices, 0.020–0.055 mm long on ABD TERG I–V and 0.025–0.060 mm long on ABD TERG VI–VIII. ABD VIII with 4 setae. SIPH with ante- and postsiphuncular sclerites (Fig. 6h). SIPH 0.30–0.41 mm, tubular, slightly tapering, straight with distinct zone of subapical reticulation and flange (Fig. 6i). Reticulated zone 0.24–0.26 \times SIPH. SIPH 1.30–2.00 \times cauda, 0.14–0.17 \times BL, and 0.32–0.41 \times ANT III. Cauda long-triangular, 0.20–0.25 mm long and 0.10–0.14 mm wide, without constriction, 1.42–2.30 \times its width at base and 0.08–0.11 \times BL with 11–12 fine setae of two lengths. Parameres triangular in ventral, flattened in ventrolateral side with rounded tips covered with numerous short, fine, pointed setae. Basal part of phallus as long as or slightly longer than parameres with numerous sensilla (Fig. 6j).

Material examined. REPUBLIC OF KOREA, Gyeonggi-do, Suwon-si, Seoul National University campus, 15 October 2000, *Picris hieracloides glabrescens*, J. Holman leg., 1 alate male, 00Ho33 (IECA); *Ixeris dentata*, 2 alate males, 00Ho25 (IECA); RDA (Yogi-San), 05 October 2000, *I. dentata*, J. Holman leg., 1 alate male, 00Ho01 (IECA); Gyeonggi-do, Suwon-si, NIAST, (Mt. Yeogi-San), 05 October 2000, *I. dentata*, J. Holman leg., 2 oviparous females, 00Ho01 (ovipara 1-2) (IECA), 2 oviparous females 00Ho01 (ovipara 3-4) (IECA), 1 apterous viviparous female, 2 oviparous females 00Ho01 (ovipara 5-7) (IECA); Gyeonggi-do, Suwon-si, Seoul National University campus, 15 October 2000, *P. hieracioidea glabrescens*, J. Holman leg., 2 oviparous females, 00Ho33 (ovipara 4-5) (IECA), 1 apterous viviparous female, 1 oviparous female, 00Ho33 (apt. 3+ovipara 1) (IECA).

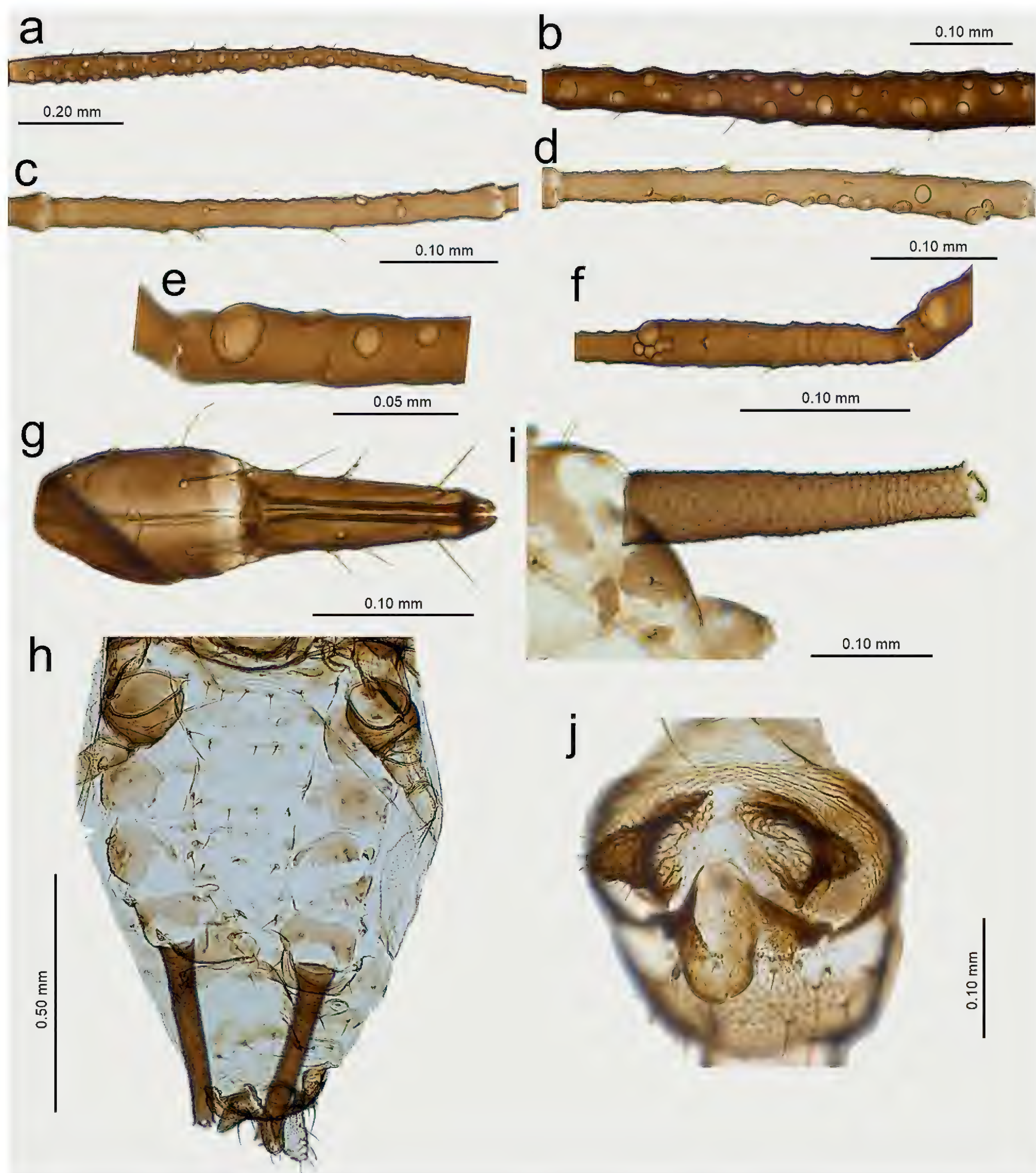


Fig. 6. Alate male of *Uroleucon formosanum*, morphological details. **a.** ANT III secondary rhinaria distribution. **b.** Secondary rhinaria structure. **c.** ANT IV secondary rhinaria distribution. **d.** ANT V secondary rhinaria distribution. **e.** Structure of primary rhinaria on ANT V. **f.** Primary rhinaria on ANT VI. **g.** Third and ultimate rostral segments. **h.** Abdomen. **i.** Siphunculus. **j.** Genitalia.

Uroleucon (Uroleucon) fuchuense (Shinji, 1942)

Figs 3, 7–9

Macrosiphum fuchuensis Shinji, 1942: 4

Dactynotus (Dactynotus) fuchuense Takahashi, 1962:75

Uroleucon fuchuense Eastop & Hille Ris Lambers, 1976: 258

Apterous viviparous females of *U. fuchuense* are characterised by a shiny salmon red to reddish brown colour in life with dark antennae, distal halves of femora, dark tib-

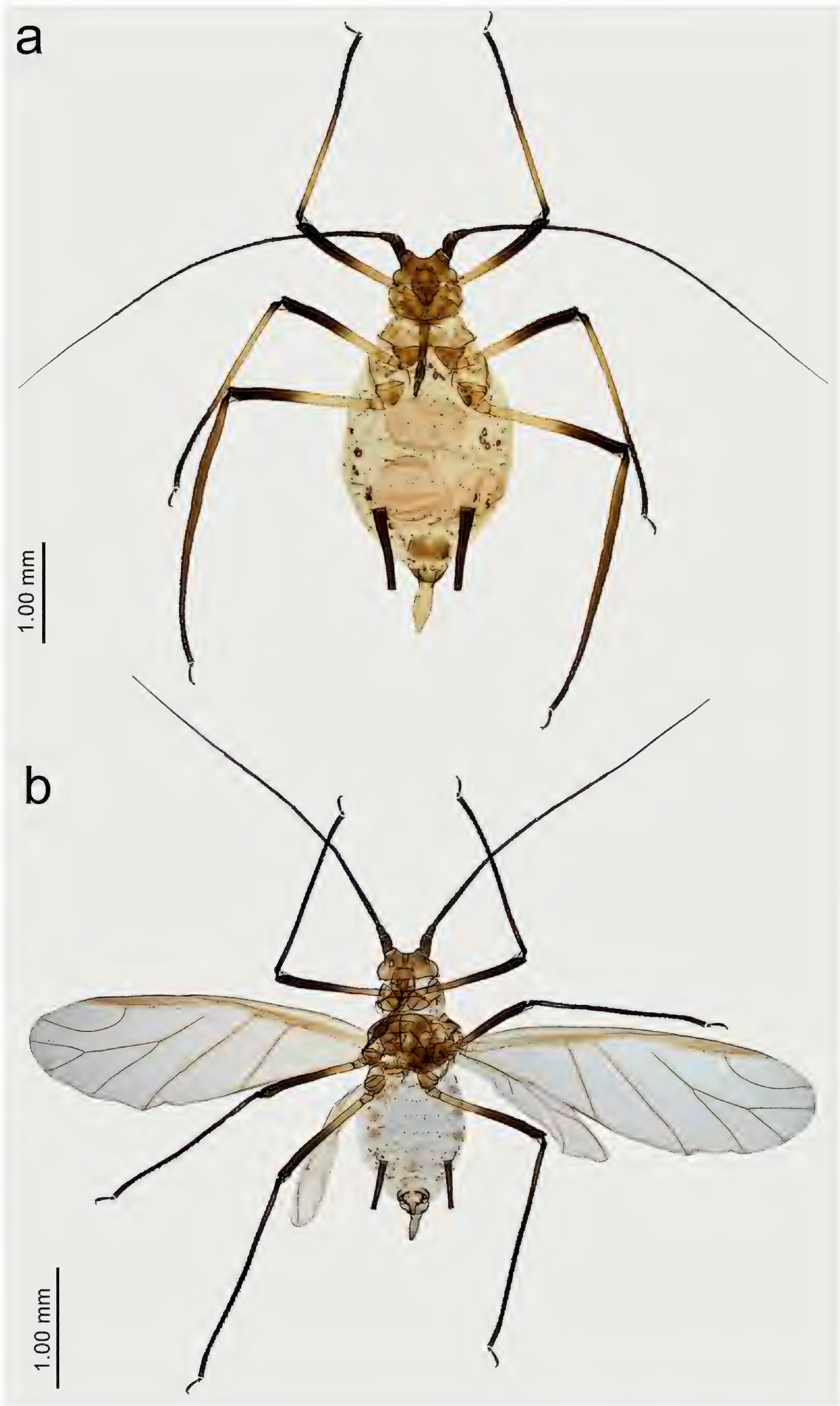


Fig. 7. Sexual morphs of *Uroleucon fuchuense*. **a.** Oviparous female. **b.** Alate male.

iae and pale cauda (Fig. 3d). Although this poorly known species is similar to *U. monticola* (Takahashi, 1935) due to the presence of a row of short, peg-like setae on the hind tibiae, it can be distinguished from it by ANT III with more than 20 secondary rhinaria, the SIPH only slightly longer than the cauda which has more than 35 setae. The species is known from Korea (Lee et al. 2002b; Choi 2019), Japan (Shinji 1941; Miyazaki 1971) and the Russian Far East (Pashchenko 1988, 2000, 2001). Miyazaki (1971) collected many apterous and alate viviparous females from *Aster scaber*. It has also been included in the review of the *Uroleucon* of Korea by Lee et al. (2002b) and *A. scaber* and *Lactuca raddeana* are the host plants. In the Russian Federation, *U. fuchuense* is known from Kamchatka and the Primorsky Krai (Pash-

chenko 2001; Pashchenko & Lobkova 1990). Although Pashchenko (2001) provided a detailed redescription of an apterous and alate viviparous female, the sexual generation was still unknown.

Oviparous female – description (n = 8)

Figs 7–8

Colour in life. Unknown. Pigmentation on slide: head brown; ANT uniformly brown with only slightly paler PT and sometimes slightly paler base of ANT III; pronotum and mesonotum usually sclerotised, brown; femora of legs yellow with dark brown distal halves; fore and middle tibiae yellow to light brown in proximal half, knee areas and distal halves dark brown; hind tibi-

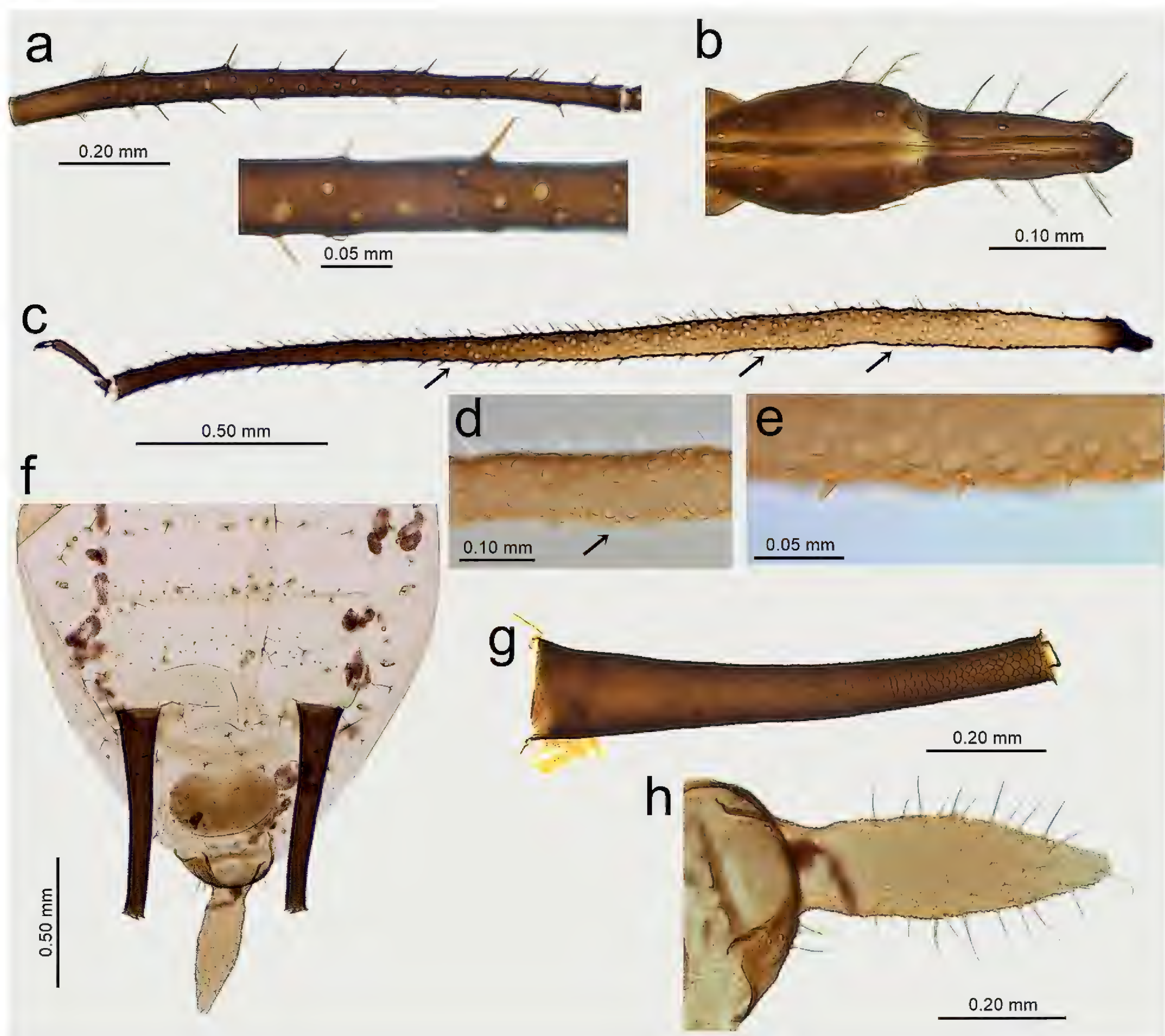


Fig. 8. Oviparous female of *Uroleucon fuchuense*, morphological details. **a.** ANT III secondary rhinaria. **b.** Third and ultimate rostral segments. **c.** Hind tibia with scent plaques and a peg-like setae distribution (arrows). **d.** Scent plaques, detailed view, and peg-like setae location (arrow) **e.** Peg-like setae, detailed view. **f.** Abdomen. **g.** Siphunculus. **h.** Cauda.

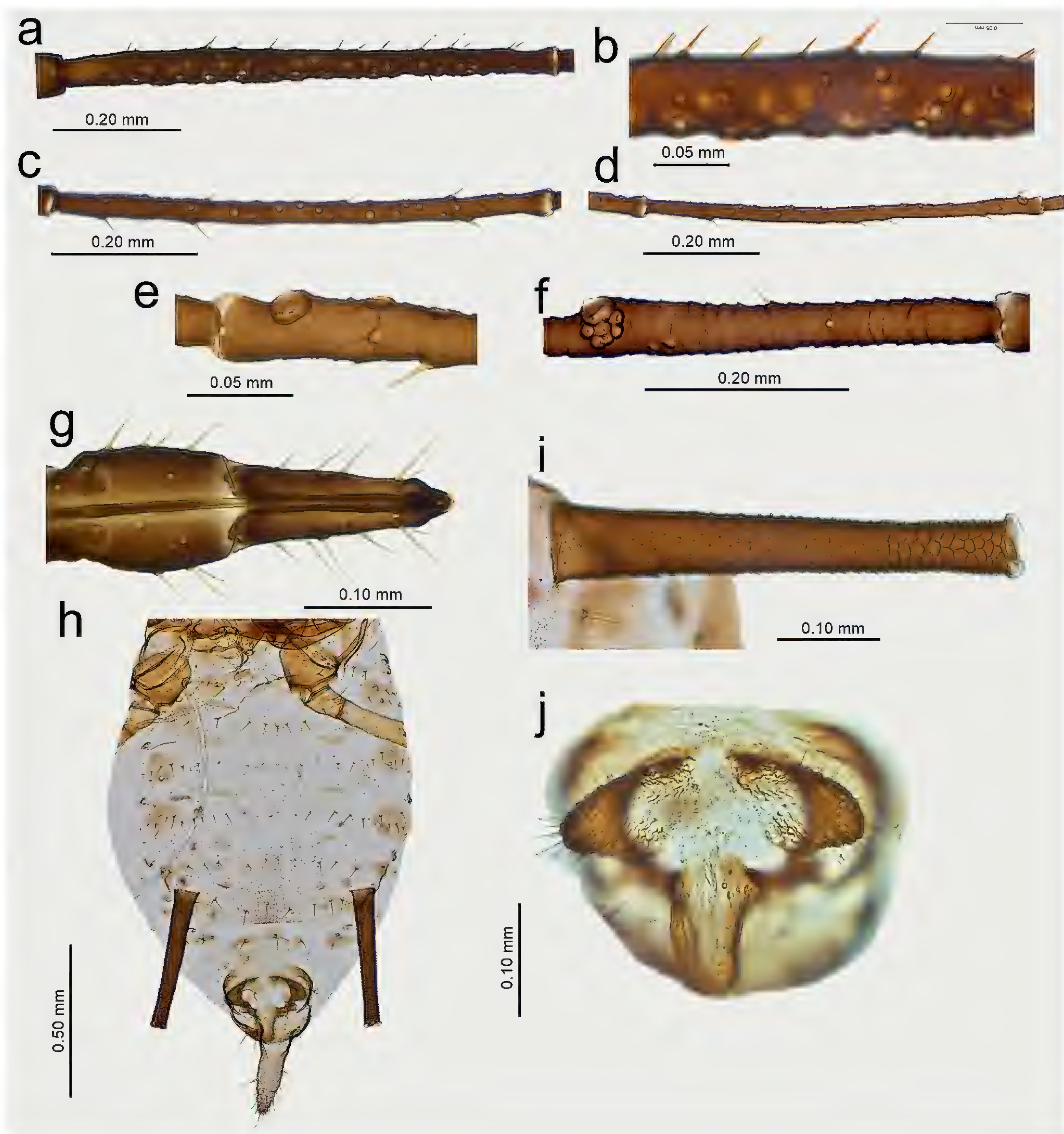


Fig. 9. Alate male of *Uroleucon fuchuense*, morphological details. **a.** ANT III secondary rhinaria distribution. **b.** Secondary rhinaria structure. **c.** ANT IV secondary rhinaria distribution. **d.** ANT V secondary rhinaria distribution. **e.** Primary rhinaria on ANT V. **f.** Primary rhinaria on ANT VI. **g.** Third and ultimate rostral segments. **h.** Abdomen. **i.** Siphunculus. **j.** Genitalia.

ae brown with paler proximal part and dark brown knee area and distal halves; tarsi dark brown; abdomen yellow with brown sclerites and scleroites; SIPH uniformly dark brown, cauda yellow (Fig. 7a).

BL 3.60–4.20 mm. HW 0.63–0.66 mm, $0.14\text{--}0.15 \times \text{ANT}$. Head with long, rigid setae with apices, 0.070–0.090 mm long. ANT tubercles each with 3 setae

on internal angles. ANT 4.20–4.41 mm, $1.05\text{--}1.16 \times \text{BL}$. ANT III 1.01–1.12 mm, with 20–26 mostly round, different-sized secondary rhinaria with very well-developed sclerotised rims (Fig. 8a), ANT IV 0.73–0.76 mm, ANT V 0.71–0.73 mm. ANT VI 1.36–1.46 mm, BASE 0.20–0.24 mm, PT 1.14–1.22 mm, $5.08\text{--}5.85 \times \text{BASE}$. Other antennal ratios: VI:III 1.26–1.34, V:III 0.64–0.72,

IV:III 0.67–0.72, PT:III 1.08–1.12, PT:IV 1.56–1.60, PT:V 1.56–1.69. ANT chaetotaxy: ANT has thick, rigid setae with mostly pointed or slightly blunt apices. ANT III setae 0.025–0.060 mm long, LS ANT III 1.00–1.33 × BD III. ANT I with 7–9, ANT II with 3–5, ANT III with 28–33, ANT IV with 16–17, ANT V with 11–12 setae. ANT VI with 3 basal, 3 apical and 8 setae along PT. Rostrum reaching hind coxae. URS 0.17–0.19 mm, 0.16 × ANT III, 0.12–0.13 × ANT VI, 0.14–0.15 × PT, 0.77–0.87 × BASE and 1.06–1.11 × HT II with 9–10 short, fine, pointed accessory setae (Fig. 8b). Mesosternal furca fused, wide without stem. III FEMORA 1.37–1.47 mm, with medium-length, thick, rigid setae with mostly pointed or slightly blunt setae, 0.025–0.065 mm long. III TIBIAE 2.62–2.80 mm, swollen in the proximal part with large number (c. 340–363) of mostly rounded or slightly irregular scent plaques (pseudosensoria) on entire area and length (except very ends) (Fig. 8c–d). III TIBIAE have rigid setae with mostly slightly pointed apices, 0.025–0.080 mm long and a row or very minute peg-like sensilla on ventral side (Fig. 8e). HT I with 5:5:5 ventral setae, HT II 0.16–0.17 mm, 0.14–0.15 × ANT III, 0.11 × ANT VI, 0.13–0.14 × PT and 0.70–0.80 × BASE. Abdomen membranous, with by well-visible mostly irregular scleroites in spinal, dorsal and marginal areas (Fig. 8f), without marginal tubercles with long, rigid setae with mostly pointed apices, 0.007–0.10 mm long on ABD TERG I–V and 0.075–0.12 mm long on ABD TERG VI–VIII. SIPH 0.72–0.81 mm, tubular, slightly tapering, slightly curved with distinct zone of subapical reticulation and flange (Fig. 8g). Reticulated zone 0.23–0.26 × SIPH. SIPH 1.20–1.22 × cauda, 0.19–0.20 × BL, and 0.71–0.72 × ANT III. SIPH surrounded by well-developed postsiphuncular sclerites. Genital plate with two anterior setae that are longer than the others, 10–14 median and 15–20 posterior setae. Cauda 0.59–0.66 mm long and 0.20–0.25 wide, tongue-shaped, slightly constricted near base, 2.64–2.95 × its width at base and 0.15–0.17 × BL with 40–44 fine setae of two lengths (Fig. 8h).

Alate male – description (n = 6).

Figs 7, 9

Colour in life. Unknown. Pigmentation on slide: head and thorax light brown to brown; ANT uniformly brown to dark brown except basal part of ANT III and ANT VI, which are usually paler; coxae brown; femora with yellow bases and brown to dark brown distal 2/3 of their length; tibiae brown with light brown to yellow section near proximal part; tarsi brown; SIPH brown; cauda pale to yellow (Fig. 7b).

2.65–3.02 mm. HW 0.56–0.59 mm, 0.14–0.16 × ANT. Head with medium-length, fine setae with pointed apices, 0.025–0.055 mm long. ANT tubercles each with 3 setae on internal angles. ANT 3.47–4.06 mm, 1.27–1.44 × BL. ANT III 0.75–0.80, with 44–65 rounded or slightly oval,

different-sized, secondary rhinaria with well-developed sclerotised rims located on entire length but not on entire surface of segment (Fig. 9a–b), ANT IV 0.60–0.80 with 12–19 secondary rhinaria mostly in one row (Fig. 9c). ANT V 0.60–0.68 mm, with 12–17 rhinaria mostly in one row (Fig. 9d). Primary rhinaria surrounded by sclerotic rim with minute projections (Fig. 9e–f). ANT VI 1.26–1.45 mm, BASE 0.18–0.22 mm, PT 1.08–1.25 mm, 5.13–6.25 × BASE. Other antennal ratios: VI:III 1.53–1.68, V:III 0.75–0.80, IV:III 0.77–0.91, PT:III 1.28–1.44, PT:IV 1.56–1.58, PT:V 1.75–1.83. ANT have short or medium-length thick, rigid setae with pointed or slightly blunt apices. ANT III setae 0.015–0.045 mm long, LS ANT III 0.87–1.12 × BD III. ANT I with 8–9, ANT II with 4–5, ANT III with 25–32, ANT IV with 12–15, ANT V with 9–10 setae. ANT VI with 3–4 basal, 3–4 apical and 5–7 setae along the PT. Rostrum reaching meso or metasternum. URS 0.17–0.18 mm, 0.19–0.22 × ANT III, 0.12–0.13 × ANT VI, 0.14–0.15 × PT, 0.77–0.94 × BASE and 1.17–1.21 × HT II with 9–11 fine, pointed accessory setae (Fig. 9g). III FEMORA 1.05–1.17 mm, bearing short to medium-length, rigid setae with pointed apices, 0.010–0.055 mm long. III TIBIAE 2.05–2.30 mm, bearing thick, rigid setae with pointed apices, 0.030–0.065 mm long. HT I with 5:5:5 ventral setae, HT II 0.14–0.15 mm, 0.15–0.18 × ANT III, 0.10–0.11 × ANT VI, 0.12 × PT and 0.63–0.77 × BASE. Abdomen membranous, with very few scleroites (Fig. 9h), small marginal tubercles on marginal sclerites on ABD II–IV (which can be poorly visible in some specimens) and with long and fine setae with pointed apices, 0.035–0.060 mm long on ABD TERG I–V and 0.050–0.080 mm long on ABD TERG VI–VIII. ABD VIII with 4 setae. SIPH 0.44–0.46 mm, tubular, straight with distinct zone of subapical reticulation and small but well-visible flange (Fig. 9i). The reticulated zone 0.21–0.26 × SIPH. SIPH 1.48–1.55 × cauda, 0.16–0.16 × BL, and 0.51–0.60 × ANT III. SIPH surrounded by ante- and postsiphuncular sclerites. Cauda 0.29–0.31 mm long and 0.12–0.16 mm wide, tapering, without constriction, 1.93–2.41 × its width at base and 0.09–0.10 × BL, with 18–24 fine, pointed setae of two lengths. Parameres robust, subtriangular in ventral, slightly flattened in ventrolateral side, with rounded tips, covered by with numerous short, fine, pointed setae. Basal part of the phallus not longer than the parameres with numerous sensilla (Fig. 9j).

Material examined. REPUBLIC OF KOREA, Gyeonggi-do, Pocheon-si, Gwangneung Royal Tomb Arboretum, 19 October 2000, *Aster scaber*, J. Holman leg., 1 alate male, 00Ho79-80 (IECA), 1 alate male, 00Ho79-80 (IECA), 1 alate male, 00Ho79-80 (IECA), 1 alate male, 00Ho79-80 (IECA), 1 alate male, 00Ho79-80 (IECA), 1 alate male, 00Ho79-80 (IECA), 1 oviparous female, 1 apterous viviparous female, 00H079-80 (IECA), 1 oviparous female, 1 apterous viviparous female, 00H079-80

(IECA), 2 oviparous females, 00H079-80 (IECA), 2 oviparous females, 00H079-80 (IECA), 2 oviparous females, 00H079-80 (IECA).

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Faunistical overview of the European species of the genera *Brachyopa* Meigen, 1822 and *Hammerschmidtia* Schummel, 1834 (Diptera: Syrphidae)

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² [urn:lsid:zoobank.org:author:C82093D8-EE58-47DD-B13A-4F47BDF73911](https://zoobank.org/urn:lsid:zoobank.org:author:C82093D8-EE58-47DD-B13A-4F47BDF73911)

³ [urn:lsid:zoobank.org:author:E40B61D9-87D8-43F9-AE84-078F10973F97](https://zoobank.org/urn:lsid:zoobank.org:author:E40B61D9-87D8-43F9-AE84-078F10973F97)

⁴ [urn:lsid:zoobank.org:author:9248DF7C-359C-4704-A999-0C67BDDAAF88](https://zoobank.org/urn:lsid:zoobank.org:author:9248DF7C-359C-4704-A999-0C67BDDAAF88)

⁵ [urn:lsid:zoobank.org:author:081B4176-2B32-43B7-BBB5-E0597FA70CD9](https://zoobank.org/urn:lsid:zoobank.org:author:081B4176-2B32-43B7-BBB5-E0597FA70CD9)

⁶ [urn:lsid:zoobank.org:author:3F9CD483-BDC2-43C5-9235-CADF874C427D](https://zoobank.org/urn:lsid:zoobank.org:author:3F9CD483-BDC2-43C5-9235-CADF874C427D)

⁷ [urn:lsid:zoobank.org:author:3299CBA9-9344-4602-9A5D-26E1BEA0D78D](https://zoobank.org/urn:lsid:zoobank.org:author:3299CBA9-9344-4602-9A5D-26E1BEA0D78D)

⁸ [urn:lsid:zoobank.org:author:7FEE17FA-2B75-4233-86C4-63B84EEC5ED0](https://zoobank.org/urn:lsid:zoobank.org:author:7FEE17FA-2B75-4233-86C4-63B84EEC5ED0)

⁹ [urn:lsid:zoobank.org:author:7CDB31C8-6B14-4514-BC20-CBC0C4B5EE29](https://zoobank.org/urn:lsid:zoobank.org:author:7CDB31C8-6B14-4514-BC20-CBC0C4B5EE29)

¹⁰ [urn:lsid:zoobank.org:author:C29560AB-7FB9-477D-B632-DF7C233981D0](https://zoobank.org/urn:lsid:zoobank.org:author:C29560AB-7FB9-477D-B632-DF7C233981D0)

¹¹ [urn:lsid:zoobank.org:author:4B94B588-FF78-404F-938C-9A89C1E49820](https://zoobank.org/urn:lsid:zoobank.org:author:4B94B588-FF78-404F-938C-9A89C1E49820)

¹² [urn:lsid:zoobank.org:author:B8F3B091-7DBF-4EFA-A002-AE3A8EAFE8B](https://zoobank.org/urn:lsid:zoobank.org:author:B8F3B091-7DBF-4EFA-A002-AE3A8EAFE8B)

¹³ [urn:lsid:zoobank.org:author:8060DF31-762D-4E61-ADB9-2B500B6B87FC](https://zoobank.org/urn:lsid:zoobank.org:author:8060DF31-762D-4E61-ADB9-2B500B6B87FC)

¹⁴ [urn:lsid:zoobank.org:author:2D994747-B04C-4A17-81F6-EBB1C2336910](https://zoobank.org/urn:lsid:zoobank.org:author:2D994747-B04C-4A17-81F6-EBB1C2336910)

¹⁵ [urn:lsid:zoobank.org:author:B695CD15-B840-4090-B872-F29F83745BBA](https://zoobank.org/urn:lsid:zoobank.org:author:B695CD15-B840-4090-B872-F29F83745BBA)

¹⁶ [urn:lsid:zoobank.org:author:4A41921E-164B-48C3-8AAF-2FCBDE7BAD5B](https://zoobank.org/urn:lsid:zoobank.org:author:4A41921E-164B-48C3-8AAF-2FCBDE7BAD5B)

¹⁷ [urn:lsid:zoobank.org:author:AD9CF66F-FDD7-42BB-821F-2C2DF8746A0F](https://zoobank.org/urn:lsid:zoobank.org:author:AD9CF66F-FDD7-42BB-821F-2C2DF8746A0F)

¹⁸ [urn:lsid:zoobank.org:author:26DF35D9-55FA-4485-8E8C-C1F90EFE1036](https://zoobank.org/urn:lsid:zoobank.org:author:26DF35D9-55FA-4485-8E8C-C1F90EFE1036)

¹⁹ [urn:lsid:zoobank.org:author:9086F7C0-622F-4E5F-BDEB-14E71A027BEE](https://zoobank.org/urn:lsid:zoobank.org:author:9086F7C0-622F-4E5F-BDEB-14E71A027BEE)

²⁰ [urn:lsid:zoobank.org:author:58B9D453-586C-4B08-BAD6-BCC606E3D654](https://zoobank.org/urn:lsid:zoobank.org:author:58B9D453-586C-4B08-BAD6-BCC606E3D654)

²¹ [urn:lsid:zoobank.org:author:59753746-8DB9-4954-A22B-6D5D582132A2](https://zoobank.org/urn:lsid:zoobank.org:author:59753746-8DB9-4954-A22B-6D5D582132A2)

²² [urn:lsid:zoobank.org:author:189149A9-D882-46F2-A5E6-FE858E7E7159](https://zoobank.org/urn:lsid:zoobank.org:author:189149A9-D882-46F2-A5E6-FE858E7E7159)

²³ [urn:lsid:zoobank.org:author:A20D5863-CF18-4BF7-BB68-0DA75D34B7A8](https://zoobank.org/urn:lsid:zoobank.org:author:A20D5863-CF18-4BF7-BB68-0DA75D34B7A8)

²⁴ [urn:lsid:zoobank.org:author:EDD44861-E7C5-4572-B487-394B2CD7C022](https://zoobank.org/urn:lsid:zoobank.org:author:EDD44861-E7C5-4572-B487-394B2CD7C022)

Abstract. The European fauna of the genera *Brachyopa* Meigen, 1822 and *Hammerschmidtia* Schummel, 1834 is reviewed. The distribution and phenology based on extensive literature and database research are provided. The biology of adults as well as larval habitats are treated. An illustrated key is presented for easy identification of the adults, including three species known from adjacent Mediterranean countries. A key to the larvae, based on the available literature, is also provided. The data originate from a study of available literature, from several databases and from the private collections of the authors. The data are compiled into one large dataset in which all the available information is gathered together with the source of the data. Based on the biology and trend analysis for each species it is indicated whether they show stable, fluctuating or extremely fluctuating populations. The habitat preferences of the adults and larvae are used to discuss possible threats to each of the species for future survival. Finally, the main habitat of all species is discussed from a conservation point of view.

Key words. Distribution, biology, habitat threats, trend analysis, identification key, larvae.

INTRODUCTION

The genera *Brachyopa* Meigen, 1822 and *Hammerschmidtia* Schummel, 1834 are found in the Holarctic and Oriental realms with 44 species of *Brachyopa* and five species of *Hammerschmidtia* currently described (Stackelberg 1952; Chu 1994; Van Steenis 2015; Skevington et al. 2019). In Europe, 20 species of *Brachyopa* and two species of *Hammerschmidtia* are known to occur (Speight 2020). Except for one species known from the Oriental realm, the occurrence of both genera is concentrated in the Nearctic subrealm and in the Mediterranean and Circumboreal region, and in the Caucasian and Manchurian provinces within the Palearctic subrealm. All these biogeographical areas are characterized by the occurrence of coniferous and deciduous, broadleaved forest (Udvardy 1975; Reemer et al. 2009; Van Steenis 2015; Skevington et al. 2019). Central Europe, as part of the Circumboreal and Mediterranean regions, harbours a high number of species and several of them are endemic to this region (Kaplan & Thompson 1981; Kassebeer 2000a, 2000c, 2001, 2002; Doczkal & Dziöck 2004; Van Steenis & Van Steenis 2014; Pérez-Bañón et al. 2016).

Adults of *Brachyopa* and *Hammerschmidtia* superficially resemble dung-flies (Scatophagidae) and some Anthomyiidae and Muscidae (Torp 1994; Rotheray 1996). They can be separated from other Syrphidae by the following combination of characters: small to medium sized (4–12 mm), rather broad, mainly brown, brown-red or black coloured flies with relatively small heads and a yellow face; postpronotum pilose; eyes bare; basoflagellomere round to oval, third antennal segment often with clearly visible sensory pit; arista subbasal, bare to long plumose; vein R_{4+5} straight; crossvein rm before middle of discal cell; vein M_1 oblique to vein R_{4+5} (Meigen 1822; Schummel 1834; Thompson & Rotheray 1998).

Larvae occur in a diverse array of microhabitats associated with tree sap runs in or within dead or living trees. Some of the species are generalists and can be found in broadleaved as well as coniferous trees, while other species seem to have a more restricted tree preference (Lundbeck 1916; Hartley 1961; McLean & Stubbs 1990; Rotheray 1991, 1996; Sivova et al. 1999; Krivosheina

2005; Dussaix 2013; Ricarte et al. 2013). Adults, and especially the males, are regularly found patrolling damaged live or dead trees with sap runs or accumulations of sap, but also on trees, tree trunks or tree logs with no visible sap runs or any other visible damage. Flower visiting is observed regularly in most *Brachyopa* species at plants with abundant, “open” and generally white coloured flowers, such as species within the families Apiaceae and Rosaceae. The flight period is from March until July (Torp 1994; Bartsch et al. 2009; Reemer et al. 2009; Bot & Van de Meutter 2019). It is not unusual to find several species of *Brachyopa* simultaneously on the same flower or around trees with supposed sap runs (e.g., Wakkie et al. 2011; Van Steenis & Van Steenis 2014; Mutin et al. 2016).

Larvae can be separated from other Syrphidae by the following characters: dorso-ventrally flattened; gradually elongating projections along lateral margin; posterior respiratory process dark, longer than broad and marked with pits and striations, four groups of sensilla anterior to anal opening (Krivosheina & Mamaev 1967; Rotheray 1996; Rotheray & Gilbert 1999; Krivosheina 2005, 2019; Pérez-Bañón et al. 2016).

Brachyopa larvae are slow-moving, possibly to avoid being detected by predators such as birds, carabid beetles and the larvae of other Diptera such as *Phaonia subventa* (Harris, 1780) (Muscidae) and *Systemus pallipes* (Von Roser, 1840) (Dolichopodidae) (Rotheray 1996). The larvae are disguised by being coated with dried sap, especially on the posterior part of the body. This sap hides the larvae from detection in the existing sap run by crypsis and possibly also by the virtual absence of gustatory and movement cues (Rotheray 1996). In general appearance they are similar to larvae of *Fannia* spp. (Fanniidae) and *Nosodendron fasciculare* (Olivier, 1790) (Coleoptera: Nosodendridae) with which they often share microhabitat. Some species can be very abundant in sap runs, with 100 larvae present in one sap-run, and some can tolerate desiccation better than others with survival after desiccation of 65% in *Brachyopa pilosa* Collin, 1939 against 95% for *Brachyopa insensilis* Collin, 1939 (Rotheray 1996).

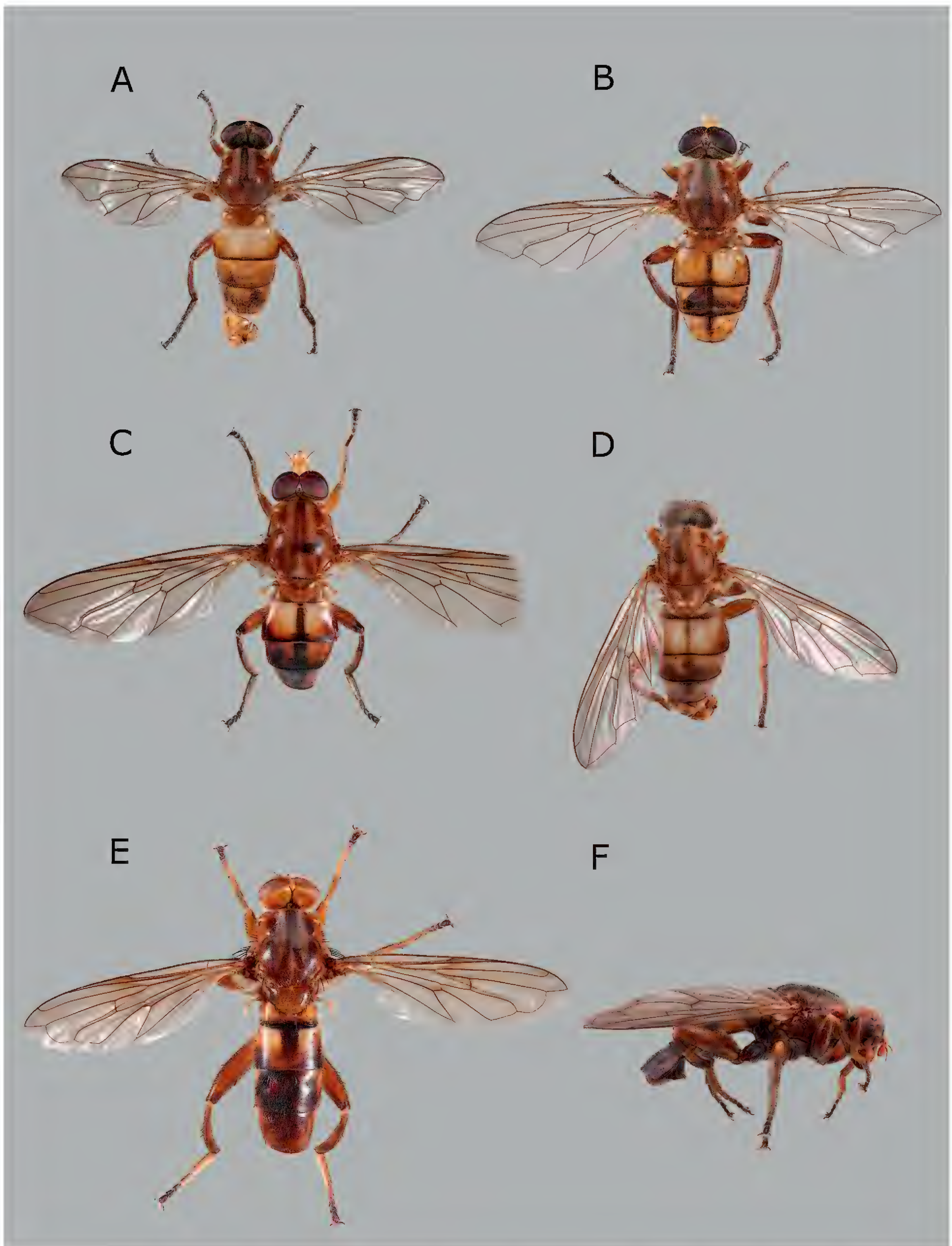


Fig. 1. Adult habitus, A–E dorsal view, F lateral view. **A.** *Brachyopa obscura*, male, Olloy-s-Viroin, Belgium. **B.** *B. testacea*, male, Engsbergen, Belgium. **C.** *B. vittata*, male, Eupen, Belgium. **D.** *B. zhelochovtsevi*, male, Tumnin, Russian Far East. **E.** *Hammerschmidtia ferruginea*, male, Fiby urskog, Sweden. **F.** *H. ingrlica*, male, Bychika, Russian Far East.

Some authors have posed the question as to whether *Hammerschmidtia* is merely a subgenus of *Brachyopa* (Vockeroth & Thompson 1987; Speight 2020). Based on recent molecular studies (Skevington et al. 2019) these genera are clearly separated and this opinion is followed here. One species, *Brachyopa (Trichobrachyopa) tristis* Kassebeer, 2001, has been placed in a different subgenus (Kassebeer 2001) but no phylogenetic studies are available to support this classification.

The European species of the genus *Brachyopa* can be separated into two subgroups based on larval morphology and ecology. One subgroup (which includes *Brachyopa dorsata* Zetterstedt, 1837, *B. panzeri* Goffe, 1945 and *B. vittata* Zetterstedt, 1843) comprises larvae with a strongly developed anal segment living in the tunnels made by other animals, mainly Coleoptera (Lymexyliidae). The other subgroup has larvae with a poorly developed anal segment which live in sap-runs or accumulations of sap under bark (Krivoshchina 2005).

Adults can be separated morphologically into three subgroups based on the colour of the scutum, the length of the arista and the presence of an antennal pit (Zetterstedt 1837; Kassebeer 2000a; Doczkal & Dziöck 2004). The first subgroup comprises all species with red-brown scutum, plumose arista and large antennal pit: *Brachyopa obscura* Thompson & Torp, 1982, *B. testacea* (Fallén, 1817), *B. vittata* and *B. zhelochovtsevi* Mutin, 1998, with possibly *B. dorsata* and *B. panzeri* also belonging to this subgroup, or maybe forming their own group. Members of the second subgroup have a grey pollinose scutum, short pilose arista and a clearly visible and sometimes very large antennal pit: *Brachyopa pilosa*, *B. plena* Collin, 1939 and *B. scutellaris* Robineau-Desvoidy, 1844. The species of the third and most species-rich subgroup have a grey pollinose scutum, bare arista and, at most, a small and weakly visible antennal pit: *Brachyopa atlantea* Kassebeer, 2001, *B. bicolor* (Fallén, 1817), *B. bimaculosa* Doczkal & Dziöck, 2004, *B. cinerea* Wahlberg, 1844, *B. grunewaldensis* Kassebeer, 2000, *B. insensilis*, *B. maculipennis* Thompson, 1980, *B. minima* Vujić & Pérez-Bañón in Pérez-Bañón et al., 2016, *B. quadrimaculosa* Thompson in Kaplan & Thompson, 1981, *B. silviae* Doczkal & Dziöck, 2004 and *B. vernalis* Van Steenis & Van Steenis, 2014. This last subgroup has previously been referred to as the *B. bicolor* group or, alternatively, the *B. quadrimaculosa* group (Kassebeer 2002; Doczkal & Dziöck 2004; Pérez-Bañón et al. 2016). Further research is needed to establish monophyly of these morphological groups.

The starting point of this paper was the initiation of the IUCN European Syrphidae Red List and the first workshop held in Novi Sad, Serbia in April 2019. For this workshop preliminary distributional data, habitat preferences and possible threats were presented as basis for further evaluation of the species. This paper gives literature as well as original, new information on distribution,

phenology and habitat preferences for the species of the genera *Brachyopa* and *Hammerschmidtia*. A short introduction is presented about population dynamics of some of the species. A literature review on habitat changes and threats is presented too. A key is presented for the known larvae and adults of the species. The key is based on literature and own observations on the adults. Each species is presented based on a fixed format with information from literature and own observations and discussion. This could be used for a final Red List assessment as required by the IUCN.

MATERIAL AND METHODS

The data presented here result from a merging of information from literature sources, online and offline databases, visits to museum collections as well as the acquisition of new data from private collections.

The terminology used and the way the specimens are measured is based on the comprehensive morphology list in Skevington et al. (2019).

For countries having a centralised database including faunistic data (e.g., Reemer et al. 2009), the data are incorporated in the central database of this study. Other resources are accessible online of which the following ones have been used for this study: Artportalen Sweden (<https://www.artportalen.se/>), Artsobservasjoner Norway (<https://www.artsobservasjoner.no/>), Diptera.info (<https://diptera.info/forum/index.php>), the Finnish Biodiversity Information Facility (<https://laji.fi/en>), Global Biodiversity Information Facility (<https://www.gbif.org/>, <https://doi.org/10.15468/dl.711aax>), Observation.org (<https://observation.org/>) including Waarneming (<https://waarneming.nl/>, <https://waarneming.be/>), National Biodiversity Network UK (<https://species.nbnatlas.org/>) and the National Biodiversity Data Centre Ireland (<https://maps.biodiversityireland.ie/Dataset/159>). The authors of this article have provided additional data from other resources that are not published or online, such as private collections, e.g., indicated as PJSA (private collection Jeroen van Steenis Amersfoort) and preliminary national checklists (e.g., Austria and Switzerland). Much additional data from literature sources is incorporated for which details are provided in the datafile rather than in the manuscript. All the literature consulted is listed in the reference section.

The following collections were visited and their records are incorporated in the database with reference to the relevant depository: FSUNS, University of Novi Sad, Faculty of Science, Department of Biology and Ecology, Novi Sad, Serbia; MEB, Museum of East Bohemia, Hradec Králové, Czech Republic; MMB, Moravian Museum, Brno, Czech Republic; MWBP, Museum of West Bohemia, Plzeň, Czech Republic; MZH, Zoological Museum Helsinki, Helsinki, Finland; NBC, Naturalis Biodiversity

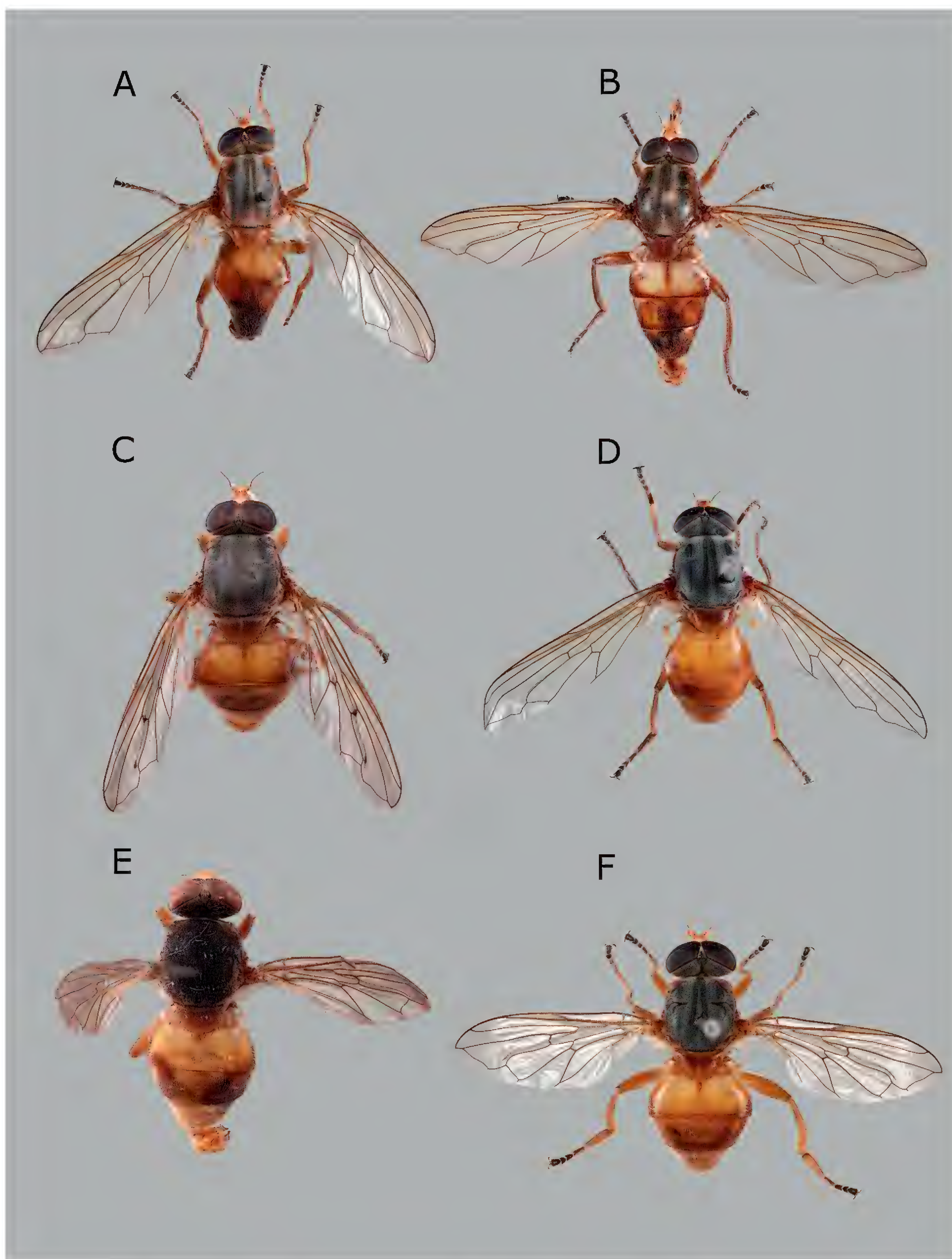


Fig. 2. Adult habitus, dorsal view. **A.** *Brachyopa dorsata*, male, Hessen, Germany. **B.** *B. panzeri*, male, Hestreux, Belgium. **C.** *B. maculipennis*, male, Fruška Gora, Serbia. **D.** *B. pilosa*, male, Drentsche Aa, the Netherlands. **E.** *B. plena*, male, Ioannina, Greece. **F.** *B. scutellaris*, male, Savelsbos, the Netherlands.

Center, Leiden, The Netherlands; NHM, Natural History Museum, London, UK; NRC, Nature Research Center, Vilnius, Lithuania; NMP, National Museum, Prague, Czech Republic; UMO, Oxford University Museum of Natural History, Oxford, UK; ZISP, Zoological Institute of the Russian Academy of sciences, Saint Petersburg, Russia; ZMSU, Zoological Museum of the Moscow State University, Moscow, Russia; ZMUC, Zoological Museum University, Copenhagen, Denmark.

The validity of several of the old literature records and some of the records from websites has not been verified by the authors. Due to name changes (Thompson 1980) and recently split species (Kassebeer 2000a; Doczkal & Dziock 2004; Van Steenis & Van Steenis 2014) several old records applied the wrong names such as *Brachyopa insensilis* and *B. bicolor* for *B. grunewaldensis* (Ricarte et al. 2013) or *B. insensilis* identified as *B. bicolor* (e.g., Claussen 1984; Kassebeer 1993). The name *B. conica* (Panzer, 1798) has been used for many species (Thompson 1980) and made the separation of *B. obscura* from *B. testacea* a puzzle (Torp 1979) until Thompson & Torp (1982) clarified this when describing *B. obscura*. The distinction of some species, especially between *B. dorsata* and *B. panzeri*, has been problematic (e.g., Reemer et al. 2007) particularly when based on photographs alone. These difficult identifications will possibly have affected some of the species distribution patterns. However, the most likely effect will be that it overestimates the common species while underestimating the rare species. This should be taken into account while reading the discussion under each species. In addition, several national Red Lists have been published and these have been discussed under each species, where relevant.

The information for each species is presented in a fixed format. The Distribution section lists the known worldwide distribution in general and the more specific European distribution. The European distribution is based on literature and own observations and we indicate if the species is here recorded as new country record. In the Biology section the information about the adult and larval biology is given. The information about biology from the literature is listed first, with all used references given, and new information is listed after. The flight period and altitudinal range are both taken from the species database and consists of information from literature and new observations. The section Population fluctuations are interpretations based on the literature, own observations and the known or suspected habitat preferences and, as such, it is a novelty of this work. The Remarks are used to highlight specific information about identification, taxonomy, explanation for its distribution or other noteworthy comments; most of this information has not been published before. The Red List section gives an overview of the published Red List status of the species in several European countries followed by a novel discussion on the possible threats for this species in Europe as a whole.

The habitat and habits of the species are taken from literature and extended by personal observations and by notes in the consulted online and offline databases. For each species the published information is given first with references, followed by the unpublished information without reference, which is referred to the main database (see below).

The names of the food plants are taken from the literature and the current name and authorship for each taxon is in line with the Plant List (WFO 2019).

Illustrations

The illustrations of pinned specimens were made using a digital SLR camera. The camera setup consisted of a Canon 6D, Canon MPE-65 macro lens, a transmitter directing two flashes and a macro rail. Helicon Focus 7.6.1 stacking software was used and photos were edited in Adobe Photoshop® 20.0.4. For the composition of the illustrations of the basoflagellomere, a similar setup was used with the addition of a Canon Extender EF 2x III and a Yongnuo YN14EX macro ring lite as light source. With the aid of a Cognisys StackShot rail, multiple pictures were taken which were stacked with Zerene Stacker 1.03. The illustrations of immature stages are taken from the literature, as acknowledged under each figure. All illustrations were further edited and assembled into the figures with GNU Image Manipulation Program 2.8.22.0.

Databasing and distribution maps

The diverse datasets available from online databases, collections, literature citations, institutional and private databases and data sheets were converted to a standardized database format designed to provide distribution maps and flight activity diagrams for this paper (referred as database hereafter).

The different coordinate systems were converted to geodetic WGS84 coordinates. If no coordinates were available in the dataset, on specimen labels or literature citations, the locality information on the label / dataset / citation was used to search Google Earth® (www.google.nl/intl/nl/earth) and GeoNames (www.geonames.org) for coordinates. In uncertain cases this was verified by searching for the coordinates through the Google search engine (www.google.com).

Some records are based on province lists. In this case, the coordinates of the centre of the province are used. Outliers on the maps were checked carefully, whether the given coordinates correlate with the label/record information.

Using records from different sources has a risk of duplicates with (slightly) different coordinates, for instance coordinates of the precise location and coordinates of the centre of the province. For the distribution maps it does not matter that much as long as duplicate records have

approximately the same coordinates, especially for areas with a high number of records. For species with fewer than 100 records, the records were checked manually: same date, observer and location description was used as an indication of a duplicate. If all information in other fields of these records supports this evidence, the derivative record was marked as a duplicate of the first record. This was also done in areas with only a few records: the Mediterranean, Ireland, Fenno-Scandia North of the Polar circle and Russia.

For the flight activity diagrams the database was queried for records of adults with a single observation datum (start date = end date). This was summed per week starting January 1st and plotted as moving average of two weeks. Outliers were checked manually and corrected or rejected when information in other fields of the record provided evidence to do so.

Altitude information from labels, literature records, databases and datasheets were used to give an altitudinal range per species. Elevations in feet were transferred to metres and all subsequent elevations are expressed in metres above sea level.

All data are included in the distribution maps, except for those marked as duplicates. The distribution maps are made in QGIS 3.10.6 with Natural EarthII (@naturalearthdata.com) as background. The country borders in the maps are from ©EuroGeographics for the administrative boundaries. Records are placed in the distribution maps in order of year of observation, with the most recent observation on top of older ones. Records with no given date are represented with a cross; records before 1950 are represented with an open symbol (white), records between 1950 and 1999 are represented with an open symbol with a central dot, and records from 2000 onwards are represented as filled symbols. Records with doubtful locality data are represented with an open symbol with a question mark.

RESULTS

Population dynamics

Only few published papers deal with the temporal dynamics of populations of the genera *Brachyopa* or *Hammerschmidtia* (Nilsson et al. 2007, 2012; Rotheray et al. 2008, 2014). Based on these papers and the known or suspected larval habitat, deductions can be made on the fluctuation in the number of populations and their density.

In the Scottish Highlands several populations of *Hammerschmidtia ferruginea* (Fallén, 1817) have been investigated and the number of populations and population sizes varied greatly over the years (Rotheray et al. 2008). In that work, authors discussed the decline and rise in number of populations from as many as 13 down

to 5, and back up to 8 over a period of 16 years. These fluctuations were caused by randomly occurring storms and coincided with the number of fallen trees, with an increase in populations after a delay of 2–5 years, each of which then lasts for 1–3 years (Rotheray & MacGowan 2000; Rotheray et al. 2014). These population fluctuations are likely to be more extreme in areas with scattered forest patches of small size, because only one locality in Scotland was found to hold stable populations when monitored from 1990 onwards (Rotheray & MacGowan 2000; Rotheray et al. 2008). The size of the forest patches with stable populations from 1990 to 2008 was between 5 and 25 ha, and the overall mean dispersal distance was measured to be 1 km, with a maximum of 5 km (Rotheray et al. 2014). A single forest with a size of more than 15 ha seems to be the lower limit for continuous survival. The number of logs is crucial for survival, and although one single fallen log can produce as many as one thousand hatched adults, the number of usable trees each year should be 3–4 at a minimum (Rotheray et al. 2008).

Similar population fluctuations have been observed for both *Brachyopa* and *Hammerschmidtia* at Stenbrohult, Djäkabygd, Sweden as well (Nilsson et al. 2007, 2012). At this 17-ha site with 7 ha of forest, *Hammerschmidtia ferruginea* and seven species of *Brachyopa* were found in large numbers between 2007 and 2010 after a storm in 2005 created suitable larval habitat. This was especially so for the species supposedly dependent upon wet decay in fallen logs or in standing dead trees, such as *Brachyopa obscura* and *Hammerschmidtia ferruginea*, both of which showed remarkably high numbers of individuals present compared to other sites in Sweden.

Species depending on sap runs on living trees (e.g., *Brachyopa bicolor*, *B. insensilis* and *B. minima*) are most likely to exhibit extreme fluctuations dependent upon the availability of suitable old trees (Sjuts 2004; Pérez-Bañón et al. 2016). In Great Britain *Brachyopa insensilis* suffered from loss of suitable larval habitat (slime fluxes on *Ulmus* spp.) due to the Dutch Elm disease causing most trees to die (Stubbs & Falk 1996). On the island of Lesbos, *B. minima* was only found on one single sap run on a *Populus nigra* L. between the years 2005 and 2011: by 2013 the tree was almost completely healed (Pérez-Bañón et al. 2016) with only a few larvae found by that time.

Another group of *Brachyopa* species (e.g., *B. dorsata*, *B. testacea* and *B. vittata*), which develop in trees with tunnels of various saproxylic insects and in tree stumps with wet decay, have a more long lived larval habitat and seem less dependent on infrequent natural storms (Löhr 1992; Krivosheina 2005). However, they are likely to benefit from the regular felling of trees during forest management, as is the case for *Blera fallax* (Linnaeus, 1758) (Rotheray & MacGowan 2015).

Some species, e.g., *Brachyopa bicolor*, have benefited strongly from massive planting of fast-growing poplars

along roads. Such trees are often pruned and inhabited by goat moth caterpillars (*Cossus cossus* Linnaeus, 1758), resulting in the frequent presence of sap runs and suitable conditions for dispersion.

Besides storms and forest management, diseases causing damage to trees can be a major factor influencing population fluctuations, as in the case of the oak dieback causing acute oak decline, Dutch Elm disease and, more recently, the bleeding canker of Horse-Chestnuts (Clouston & Stansfield 1979; Führer 1998; Thomas 2008; de Keijzer et al. 2012; Denman et al. 2014; Denman et al. 2018).

Habitat changes and threats

The species of the genera *Brachyopa* and *Hammerschmidtia* are highly dependent on a very specific larval habitat, namely senescent trees with sap runs or recently fallen tree trunks and stumps with a buildup of decaying sap. The adults are often found near the larval habitat and feed on various flowering herbs, shrubs and trees. The population size will probably be restricted by the availability of suitable larval habitat, but perhaps the availability of a nearby adult food source may also play a role in maintaining healthy populations (Fayt et al. 2006). Several species are known to visit flowers frequently and are likely to be able to fly long distances.

Both the quality and quantity of resources, e.g., the number of senescent trees and the surface of the forested area, are probably the most important factor influencing the population size of the species. The changes in European forest dynamics and de- or re-forestation have been thoroughly investigated (Kaplan et al. 2009; Taff et al. 2009; Hughes et al. 2012). Forest cover has changed considerably over time, leading to a net decrease of ancient forest throughout Europe. Broadleaved floodplain forests, swamp forests of different kinds and some Macaronesian and Mediterranean forests are most severely threatened. The central European alluvial and swamp forests have been lost due to the regulation of rivers and changes in hydrology, with possibly only 5% preserved in small remnants (Hughes et al. 2012; Potapov et al. 2012; Birks et al. 2016; European Commission 2016; Zanon et al. 2018). In some West-European countries, however, the forested area is recovering and forest management has changed in ways that favour Syrphidae (Reemer 2005; Fuller et al. 2013).

In Europe, small areas with primaeval forest remain in Fennoscandia, Poland, Portugal and the alpine countries, while in South-Eastern Europe larger areas still have untouched forest (Sabatini et al. 2018; Jaroszewicz et al. 2019). Many of these forest remnants are not protected, and even those that are protected are threatened by logging activities and large infrastructure development (Jaroszewicz et al. 2019; McGrath 2019). Meanwhile, in Eastern Europe there are reports of reforestation

due to changing land use. People are moving from the countryside to cities and the abandoned fields eventually become overgrown with trees. However, the intensive management of the forest has also ceased in many places, influencing the forest composition and possibly in some cases causing a deterioration of adult (loss of flowering plants due to abandoning fields) and even the larval habitat (Alix-Garcia et al. 2016; Gutman & Radelof 2017; Prokopová 2018). Commercial forests tend to have a monoculture of tree species with few flowering herbs and shrubs as potential adult food sources. In more open agricultural landscapes, these flowering plants are still available but solitary old trees are being removed in an increasingly way. These two effects result in a spatial mismatch between larval and adult habitat, likely to lead to a decrease in population size and eventually also in the number of populations (de Foresta et al. 2013; Scherber et al. 2014; Felton et al. 2016; Liu et al. 2018).

Traditionally oak (*Quercus* sp.) has been widely managed and used for a variety of purposes, such as bark for tanning, wood for construction and mining, glass production and forest pasture for livestock. In the absence of traditional forestry practices, such as coppicing with standards, most oak and oak-hornbeam forest undergoes a natural succession to beech-dominated forest in which ancient oak trees with sap runs disappear. This loss can be exacerbated by modern forestry practices in which all trees are harvested at the same time (Bobiec et al. 2018; Mölder et al. 2019). However, it has also been suggested that the natural succession to beech could possibly be suppressed by diseases causing a (recent) decline in beech populations (Jung 2009).

Other threats to the forest come from deposition of nitrogen, carbon dioxide and pesticides (Bleeker & Erisman 1998; Wamelink et al. 2009; van Dobben & de Vries 2017; Zou & Knops 2018) disturbing the natural balance within the forest and causing multifaceted effects. The effects have not been studied in detail for Syrphidae, but it seems that nitrogen and carbon dioxide influence floral growth rate in such a way that trees tend to age faster (Erisman et al. 2014; Vogels et al. 2017; Wallis de Vries & Bobbink 2017; EEA 2018). This could, temporarily, increase the larval habitat. A recent study, however, showed a negative impact on pollinators as a response to increased deposition of nitrogen (Carvalho et al. 2020). Insecticides and fungicides on the other hand have a strong negative influence on larval development and adult fecundity in aphidophagous Syrphidae (Colignon et al. 2003). It is highly likely these pesticides will also have a negative influence on saproxylic species like in the genera *Brachyopa* and *Hammerschmidtia*.

Finally, global climate change has a great impact on the natural world and forest composition, which in turn will have a great effect on its fauna (Ramsfield et al. 2016; Morin et al. 2018; Pureswaran et al. 2018; Jactel et al. 2019; Jandel et al. 2019). These effects are even more

complex than those from nitrogen or pesticide deposition and are increasingly being investigated for Syrphidae. These studies (Radenković et al. 2017; Miličić et al. 2018; Milić et al. 2019) show that different species have different responses, ranging from extensions in range, to declines and even extinction. The dispersal capability of each species and especially the dispersion of the habitat of that species are factors not easily accounted for and thus range extension is not only related to climate change per se, but mostly to habitat change (Warren et al. 2001; Schweiger et al. 2012; Fourcade et al. 2017; Milić et al. 2019). The most remarkable conclusion was that this could lead to a decrease in lowland species richness (Roth et al. 2014; Miličić et al. 2018; Milić et al. 2019), which in turn could lead to an increased decline of already rare species due to possible increased competition from commoner species (Warren et al. 2001).

It is clear that the forests and woodlands of Europe are threatened in many ways and that protective measures are needed to ensure their future survival and the flora and fauna dependent upon them. The EU (2016) list of threatened habitats is a good example of what is needed for this protection. Under each Syrphidae species the threat category of the habitat, given in the codes of the EUNIS (EUropean Nature Information System) habitat classifications of Woodlands, is discussed based on the information from this Red List.

Key to the adults of the European and circum Mediterranean species of *Brachyopa* and *Hammerschmidtia*

- 1 Vein M_1 perpendicular to vein R_{4+5} and abdomen straight, almost parallel-sided (Fig. 1E); all femora enlarged, clearly thicker than 2.2 times the width of tibiae; metatibia with short stout black setae posteromedially (Fig. 16G); male with tuberculate face (Figs 8E, 8F) ... *Hammerschmidtia* Schummel
- Vein M_1 ending oblique to vein R_{4+5} and abdomen conical, widest at posterior part of tergum II, gradually and clearly narrowing towards posterior tip of abdomen (see Figs 1A–C); femora only slightly enlarged and not much wider than 1.5 times the width of tibiae; metatibia with only normal short pile; male and female without facial tubercle (see Figs 8A–D) *Brachyopa* Meigen

Hammerschmidtia key

- 1 Arista plumose (Fig. 19E); katapisternum with dorsal and ventral pile patch, in female dorsal patch consisting of very few pili; postero-ventral part of katapisternum with long, strong, black setae; apex of profemur anteriorly with 1–4 strong, long yellow or black setae (Fig. 16F); apex of mesofemur posteriorly with 3 long and very strong, black setae, more than

3 times longer than other black setae; large species 11–15 mm

..... *Hammerschmidtia ferruginea* (Fallén, 1817)

- Arista short pilose and pile no longer than 3 times the diameter of arista at base (Fig. 19F); katapisternum with ventral pile patch and sometimes some white pile on postero-dorsal corner; postero-ventral part of katapisternum only with normal white pile; apex of profemur anteriorly without strong, long yellow or black setae; apex of mesofemur posteriorly with 3 rather long and strong, black setae, at most 2 times longer than other black setae; smaller species 8–11 mm *Hammerschmidtia ingraca* Stackelberg, 1952

Brachyopa key

Not all species were available and the key is adjusted based on the studied material and the following literature: Kassebeer (2000a, b, 2001, 2002), Doczkal & Dziöck (2004), and Pérez-Bañón et al. (2016). All the species from the circum Mediterranean region including North Africa and Turkey are incorporated here as well since they could occur in Europe too. The genitalia of several species of *Brachyopa* have been illustrated by Pellmann (1998), for each of these species this is indicated by “*GP” indicating the * sign as remark and GP as genitalia Pellmann (1998). Most of the missing species in Pellmann (1998) have been illustrated in the papers in which the species were published for the first time (e.g., Thompson & Torp 1982; Mutin 1998; Kassebeer 2001; Van Steenis & Van Steenis 2014).

- 1 Frons bulging, clearly visible above the eyes in lateral view; face very wide; subscutellar pile fringe well developed; proepimeron pilose; length 12.7 mm *Brachyopa (Trichobrachyopa) tristis* Kassebeer, 2001 (Only known from its type locality in Algeria)
- Frons flat, hardly visible above the eyes; face narrow; subscutellar fringe at most poorly developed; proepimeron at most with a few pili; smaller species 2 (*Brachyopa* sensu stricto)
- 2 Arista pilose to bare, length of pile at most 1.5 times longer than width of basal part of arista (Figs 20–21); scutum and pleura blueish-grey with black ground colour (see Figs 2C–F) or brown-reddish (Figs 2A, 2B) 6
- Arista plumose, length of pile at least 2 times longer than width of basal part of arista (Figs 19A–D); scutum and pleura almost entirely brown-reddish (see Figs 1A–D) 3
- 3 Arista long plumose, pile more than 3 times longer than width of basal part of arista (Fig. 19C); katapisternum with dorsal and ventral pile patch;

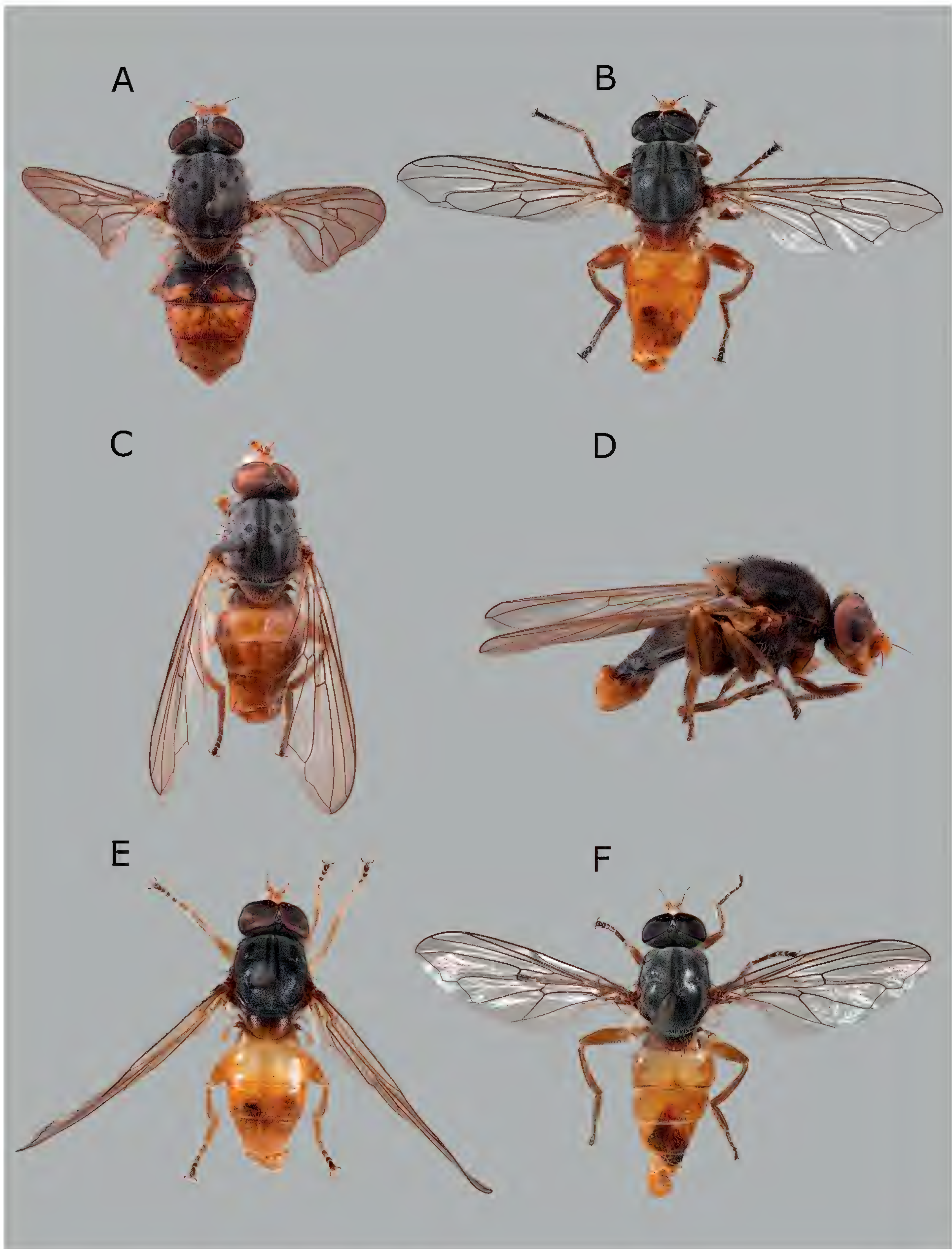


Fig. 3. Adult habitus, A-C, E, F dorsal view; D lateral view. **A.** *Brachyopa atlantea*, female, Granada, Spain. **B.** *B. bicolor*, male, Engsbergen, Belgium. **C.** *B. bimaculosa*, male, Bolgenachtal, Germany. **D.** *B. cinerea*, male, Komsomolsk-na-Amur, Russian Far East. **E.** *B. grunewaldensis*, male, Arkadia, Greece. **F.** *B. insensilis*, male, Diest, Belgium.

- face strongly produced antero-ventrally; posterior anepisternum with 4–10 long strong black setae; post-alar callus with long and strong black setae-like pile mixed with light-yellow pile, black pile almost twice as long as pile on scutum; length 8–11 mm
.....*Brachyopa vittata* Zetterstedt, 1843 *GP
- Arista short plumose, pile at most 3 times longer than width of basal part of arista (Figs 19A, 19B, 19D); katepisternum with ventral pile patch only; face weakly to slightly produced antero-ventrally; posterior anepisternum with at most 3–5 rather long, black setae; post-alar callus with yellow or mixed yellow and black pile, black pile only slightly longer and stronger than pile on scutum 4
- 4 Face rather strongly produced antero-ventrally (Fig. 8D); katepisternum and meron brown-reddish, same colour as rest of pleura; sensory pit narrow, longer than wide, tapering towards ventral margin; arista rather long pilose, pile 2–3 times larger than diameter of arista at base (Fig. 19D); length 6.0–7.5 mm*Brachyopa zhelochovtsevi* Mutin, 1998
- Face only slightly produced antero-ventrally (Figs 8A, 8B); in males at least ventral half of katepisternum and meron dark-brown to black, contrasting with brown-reddish rest of pleura; sensory pit small and circular; arista long or short pilose (Figs 19A, 19B) 5
- 5 Abdomen with medial black vitta on terga II–IV (Fig. 1B); face produced antero-ventrally (Fig. 8B); arista longer pilose, pile almost 3 times longer than width of arista basally (Fig. 19B); length 6.5–8.0 mm*Brachyopa testacea* (Fallén, 1817) *GP
- Abdomen without medial black vitta on terga II–IV (Fig. 1A); face weakly produced antero-ventrally (Fig. 8A); arista rather short pilose, pile about 2 times longer than basal width of arista (Fig. 19A); length 5–7 mm
.....*Brachyopa obscura* Thompson & Torp, 1982
- 6 Arista virtually bare and sensory pit on basoflagellomere at most weakly developed small and round (Figs 20C, 21) 11
- Arista pilose, pile at least as long as width of arista and sensory pit on basoflagellomere clearly developed, round or oval to large kidney shaped (Figs 20A–B, 20D–F) 7
- 7 Scutum and pleura greyish, blue-grey pollinose with weaker pollinose pattern (Figs 2C–D) 9
- Scutum and pleura reddish-brown, brownish pollinose with extensive shiny pattern (Figs 2A, 2B) 8
- 8 Posterior margin of scutellum with long black bristles, 2–4 times longer than pile in the middle of scutellum; scutellar disc extensively pollinose medially and anteriorly; sensory pit as small as diameter of arista at base (Fig. 20A); postero-dorsal corner of anepisternum with some black setae; length 6–9 mm*Brachyopa dorsata* Zetterstedt, 1837 *GP
- Posterior margin of scutellum without long black bristles; scutellum only anterior margin narrowly pollinose; sensory pit large, more than 2.5 diameter of arista at base (Fig. 20B); anepisternum with only white pile; length 6–9 mm
.....*Brachyopa panzeri* Goffe, 1945 *GP
- 9 Postpronotum and post-alar callus blackish, same colour as scutum and tergum II with at most a few black pili on posterolateral margin (Fig. 2D); frons in male more narrowly pollinose (Fig. 13C); length 6–8 mm*Brachyopa pilosa* Collin, 1939 *GP
- Postpronotum and post-alar callus orange-brownish, lighter than scutum and tergum II extensively black pilose postero-lateral margin (Figs 2E, 2F); frons in male broadly pollinose (Figs 13D, 13E) 10
- 10 Sensory pit on basoflagellomere small, rounded (Fig. 20E); scutellar disc rather long pilose, pile length about half as long as posterior scutellar setae; length 7–8 mm*Brachyopa plena* Collin, 1939
- Sensory pit on basoflagellomere large, kidney-shaped (Fig. 20F); scutellar disc rather short pilose, pile length at most 1/3 as long as posterior scutellar setae; length 6–8 mm
.....*Brachyopa scutellaris* Robineau-Desvoidy, 1844 *GP
- 11 Abdomen shiny black, antennae, face, scutellum and male genitalia orange-yellow (Fig. 3D); length 6–8 mm*Brachyopa cinerea* Wahlberg, 1844
- Abdomen reddish, often with dark-brown to black markings, scutellum and genitalia greyish (Figs 3A–C, 3E–F, 4) 12
- 12 Wing with two small black maculae and postpronotum dark-orange, lighter than rest of scutum (Fig. 2C); length 7.0–9.5 mm
.....*Brachyopa maculipennis* Thompson, 1980 *GP
- Wing hyaline and postpronotum dark brown, greyish pollinose, same colour as rest of scutum (Figs 3A, 3B, 3E, 3F, 4) 13
- 13 Notopleural sulcus at most weakly developed; scutellum with a distinct transverse depression and with distinct patch of microtrichia at base; protarsus entirely black; metafemur enlarged; basoflagellomere with distinct sensory pit (Fig. 21B); length 6–9 mm
.....*Brachyopa bicolor* (Fallén, 1817) *GP
- Notopleural sulcus well developed; scutellum without transverse depression; protarsus mixed black and yellow coloured; mesofemur less clearly

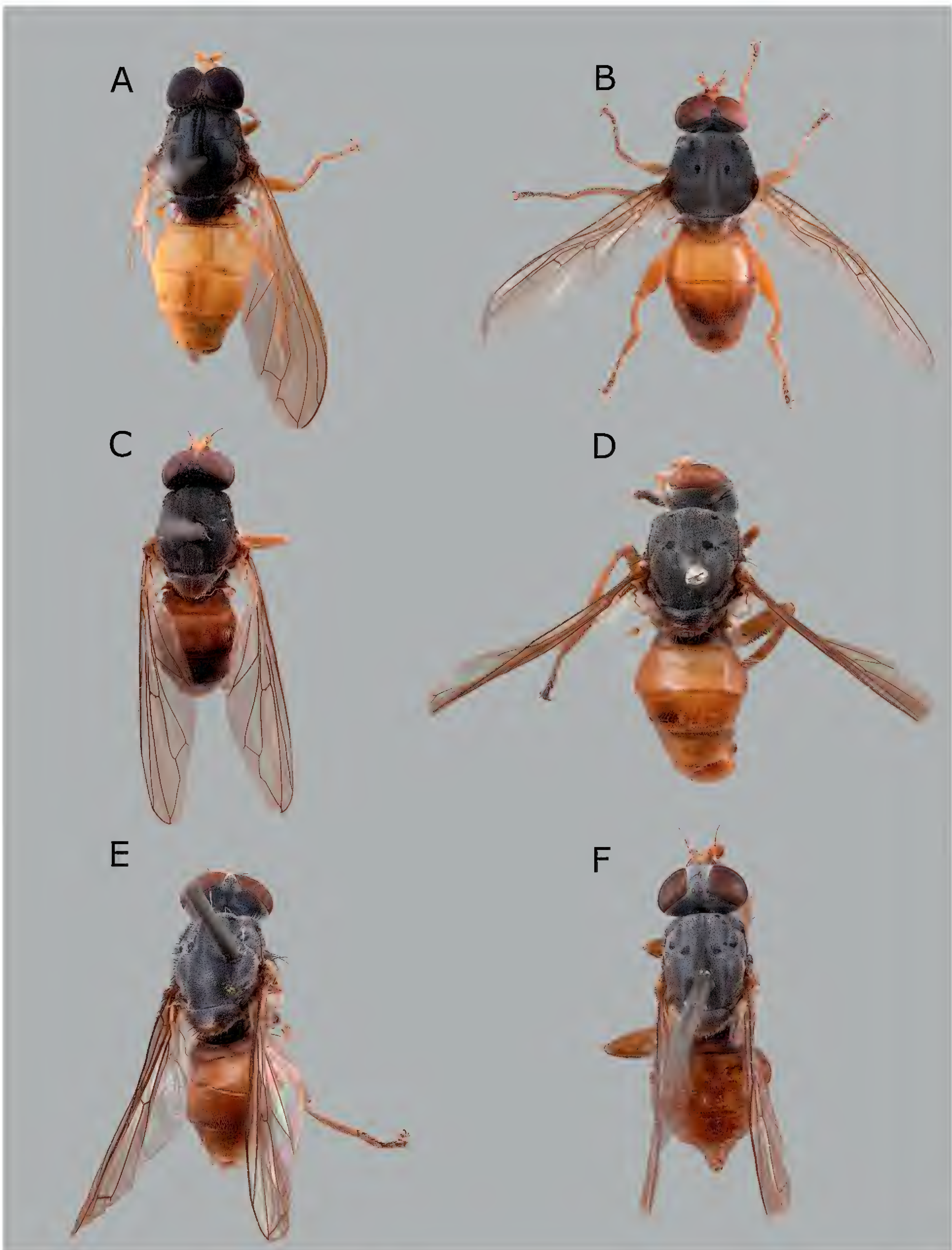


Fig. 4. Adult habitus, dorsal view. **A.** *Brachyopa cruriscutum*, male paratype, Hakkari, Turkey. **B.** *B. silviae*, male, Bringhausen, Germany. **C.** *B. minima*, male, Lesvos, Greece. **D.** *B. vernalis*, male paratype, Crete, Greece. **E.** *B. quadrimaculosa*, male, Samos, Greece. **F.** *B. quadrimaculosa*, female, Samos, Greece.

- enlarged; basoflagellomere with at most a weak sensory pit (Figs 21A, 21C, 21E, 21F) 14
- 14 Scutum (Fig. 4A) and vertical triangle (Fig. 15A) extensively shiny, black with weak coverage of blue-greyish microtrichia; length 6–7 mm
Brachyopa cruriscutum Van Steenis & Van Steenis, 2014
- Scutum and vertical triangle almost entirely to entirely covered with blue-greyish microtrichia (Figs 4B–F, 14, 15B–D) 15
- 15 Scutum microtrichose except for 2 or more clear black shiny maculae, bare of microtrichia (Figs 3A, 3C, 4B, 4D–F); postalar callus entirely microtrichose or with medial part bare and shiny 17
- Scutum entirely covered with microtrichia (Figs 3E, 3F); postalar callus microtrichose, with medial part bare and shiny 16
- 16 Protarsus almost entirely dark-brown to black coloured (Fig. 3F); ocellar triangle entirely greyish pollinose (Fig. 14E); mouth-edge rather strongly protruding (Fig. 10F); length 6.0–8.5 mm
Brachyopa insensilis Collin, 1939 *GP
- Protarsus with tarsomeres bicoloured, basal part yellow apical part dark-brownish (Fig. 3E); ocellar triangle weakly pollinose, with shiny black pattern (Fig. 14D); mouth-edge only weakly protruding (Fig. 10E); length 7.0–8.5 mm
Brachyopa grunewaldensis Kassebeer, 2000
- 17 Halter entirely yellow 19
- Halter yellow except for capitulum which is partly dark-greyish (see Fig. 4D) 18
- 18 Face yellow with black triangular fascia between eyes and antennae (vaguely visible in Fig. 11D); proleg with tarsomere 1 yellow, tarsomeres 2–3 dark-brown with broad yellow apical margin, and tarsomeres 4–5 entirely dark-brown; posteroventral corner of anterior anepisternum nearly entirely microtrichose, at most a tiny bare macula; length 5.5–7.5 mm
Brachyopa vernalis Van Steenis & Van Steenis, 2014
- Face yellow, mouth edge narrowly black (Figs 11E, 11F); proleg with tarsomeres 1–5 entirely dark-brown; posteroventral corner of anterior anepisternum with shiny macula, bare of microtrichia; length 6–8
Brachyopa quadrimaculosa Thompson, 1981
- 19 Postalar callus with medial part bare and shiny ... 21
- Postalar callus entirely microtrichose 20
- 20 Scutum with one pair of round bare shiny maculae at the transverse suture (Fig. 3C); hypostomal bridge yellow (Fig. 10C); ocellar triangle densely covered with microtrichia, not shiny (Fig. 14B); ventral scutellar fringe absent; sterna entirely pollinose; length 6–8 mm
Brachyopa bimaculosa Doczkal & Dziok, 2004
- Scutum with one pair of triangular bare shiny maculae at the transverse suture (Fig. 4B); hypostomal bridge blackish (Fig. 11B); at least centre of ocellar triangle bare of microtrichia, shiny black; ventral scutellar fringe present; more than half of the surface of sterna 3 and 4 non-pollinose; length 7–8 mm
Brachyopa silviae Doczkal & Dziok, 2004
- 21 Wing with dark-brown macula on vein r-m; medial end of transverse suture with brownish pollinose macula; scutellum entirely orange-brown; length 6.5 mm
Brachyopa tabarkensis Kassebeer, 2002
- Wing hyaline (Figs 3A, 4C); medial end of transverse suture with non-pollinose, shiny black macula (Fig. 3A) or grey pollinose like the other pollinosity of the scutum; scutellum orange-brown with dark-brown anterior margin 22
- 22 Medial end of transverse suture with non-pollinose, shiny black macula (Fig. 3A); length 6–8 mm
Brachyopa atlantea Kassebeer, 2000
- Medial end of transverse suture pollinose; length 6–7 mm
Brachyopa minima Vujić & Pérez-Bañón, 2016

Key to the known third-instar larvae of the European species of *Brachyopa* and *Hammerschmidtia*

(Based on Krivosheina & Mamaev 1967; Rotheray 1996; Rotheray & Gilbert 1999; Kassebeer 2000a; Krivosheina 2003; Krivosheina 2005, 2019; Pérez-Bañón et al. 2016)

- 1 Posterior respiratory process (prp) relatively short, protruding only slightly beyond last pair of anal lappets (Fig. 5C); anal lappets of nearly equal length; dorsal part of abdomen evenly coated in setae, not forming “transverse rows”; abdominal segments 2–6 with oblique furrow, separating the medial from the dorsal sensilla
Hammerschmidtia Schummel
- PRP relatively long, protruding strongly beyond last pair of anal lappets (Fig. 5A); anal lappets of unequal length, becoming increasingly shorter posteriorly; dorsal part of abdomen with either transverse rows of setae or coated in blotches; abdominal terga 2–6 without oblique furrow, the medial and dorsal sensilla not separated from each other
Brachyopa Meigen

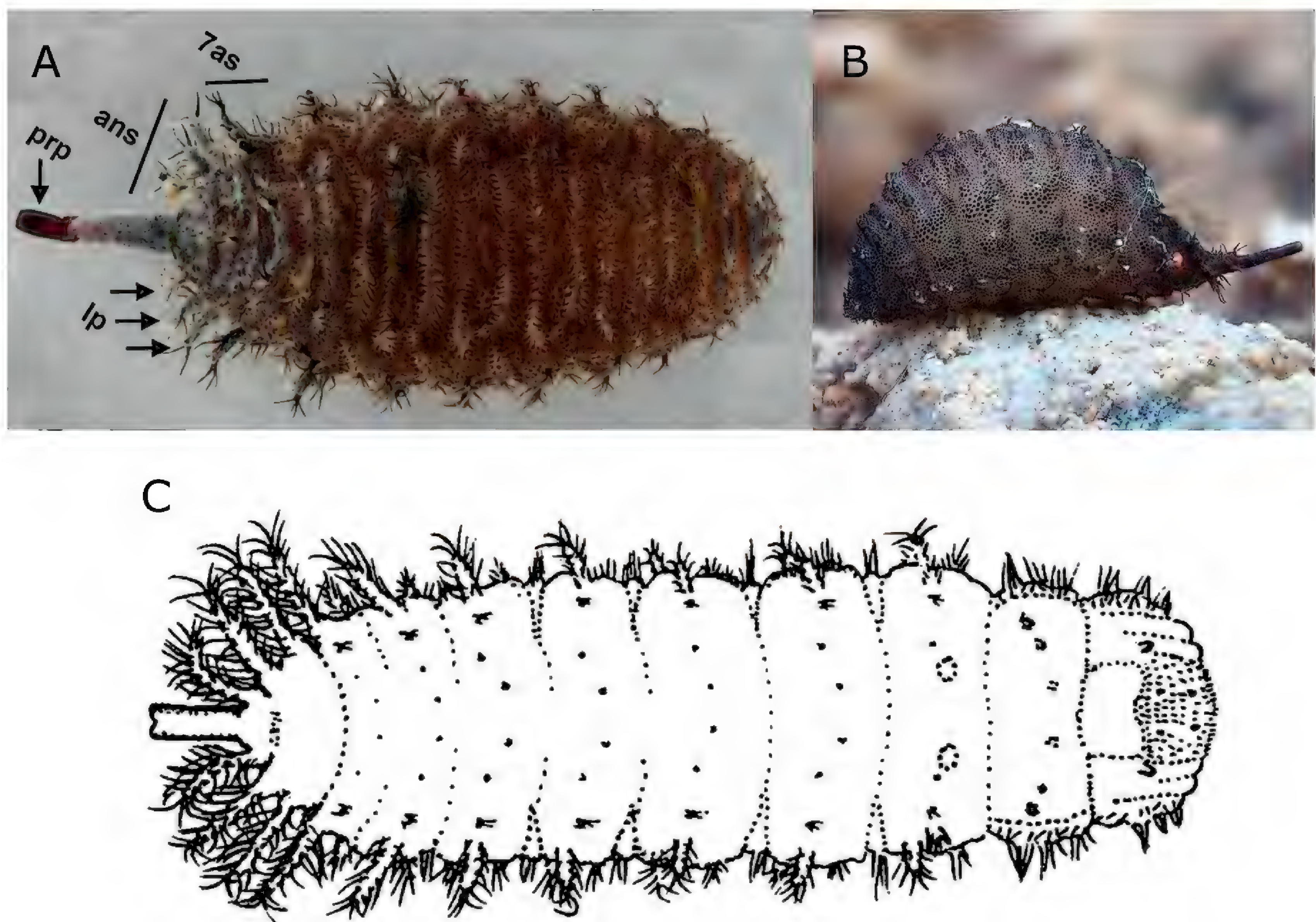


Fig. 5. Third instar larva and pupa. **A.** *Brachyopa bicolor*, larva, after Pérez-Bañón et al. 2016. **B.** *Brachyopa insensilis*, pupa, Brussels, Belgium, photo B. Wakkie. **C.** *Hammerschmidtia ingrlica*, larva, after Krivosheina 2003. Abbreviations: 7as = 7th abdominal segment; ans = anal segment; lp = lappets; prp = posterior respiratory process.

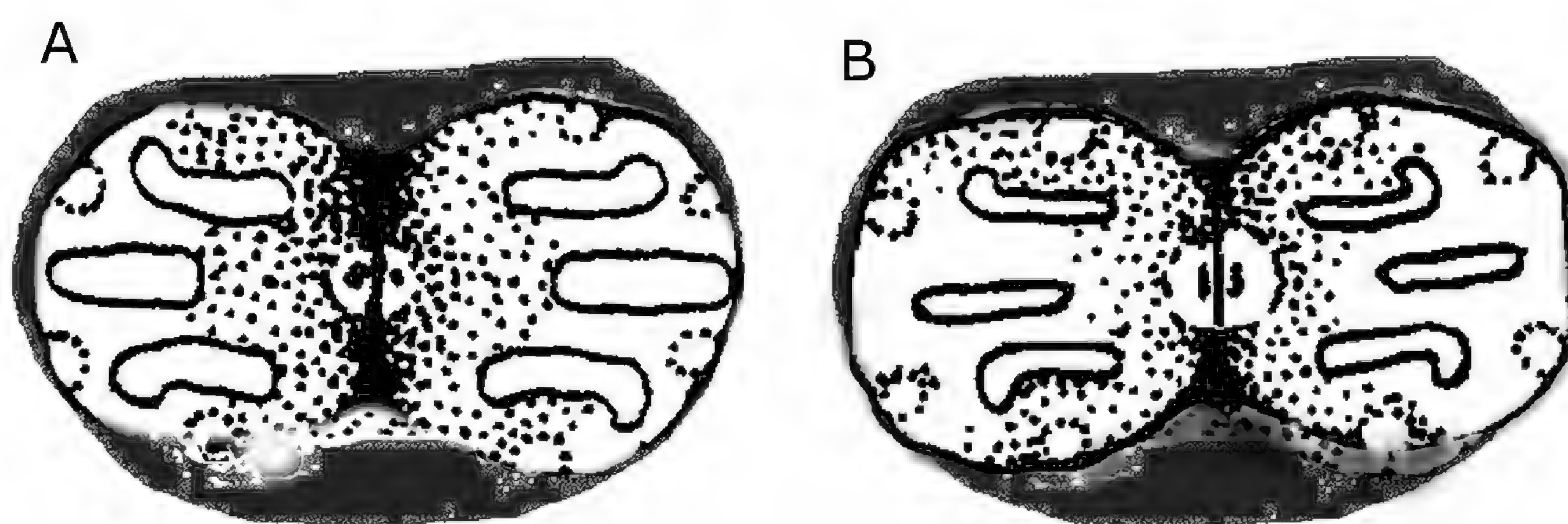


Fig. 6. Posterior respiratory process, after Krivosheina 2003. **A.** *Hammerschmidtia ferruginea*. **B.** *Hammerschmidtia ingrlica*.

Key to the larvae of the European species of *Hammerschmidtia*

- 1 Posterior respiratory process (prp) with three pairs of spiracular openings, length about half the width of the prp, the lateral pairs strongly bent, the medial

- pair ending close to the lateral margin of the prp (Fig. 6A) *Hammerschmidtia ferruginea* (Fallén)
- PRP with openings shorter, about 1/3 of the width of the prp, lateral respiratory opening more straight, the medial pair further away from the lateral margin (Fig. 6B) *Hammerschmidtia ingrlica* Stackelberg

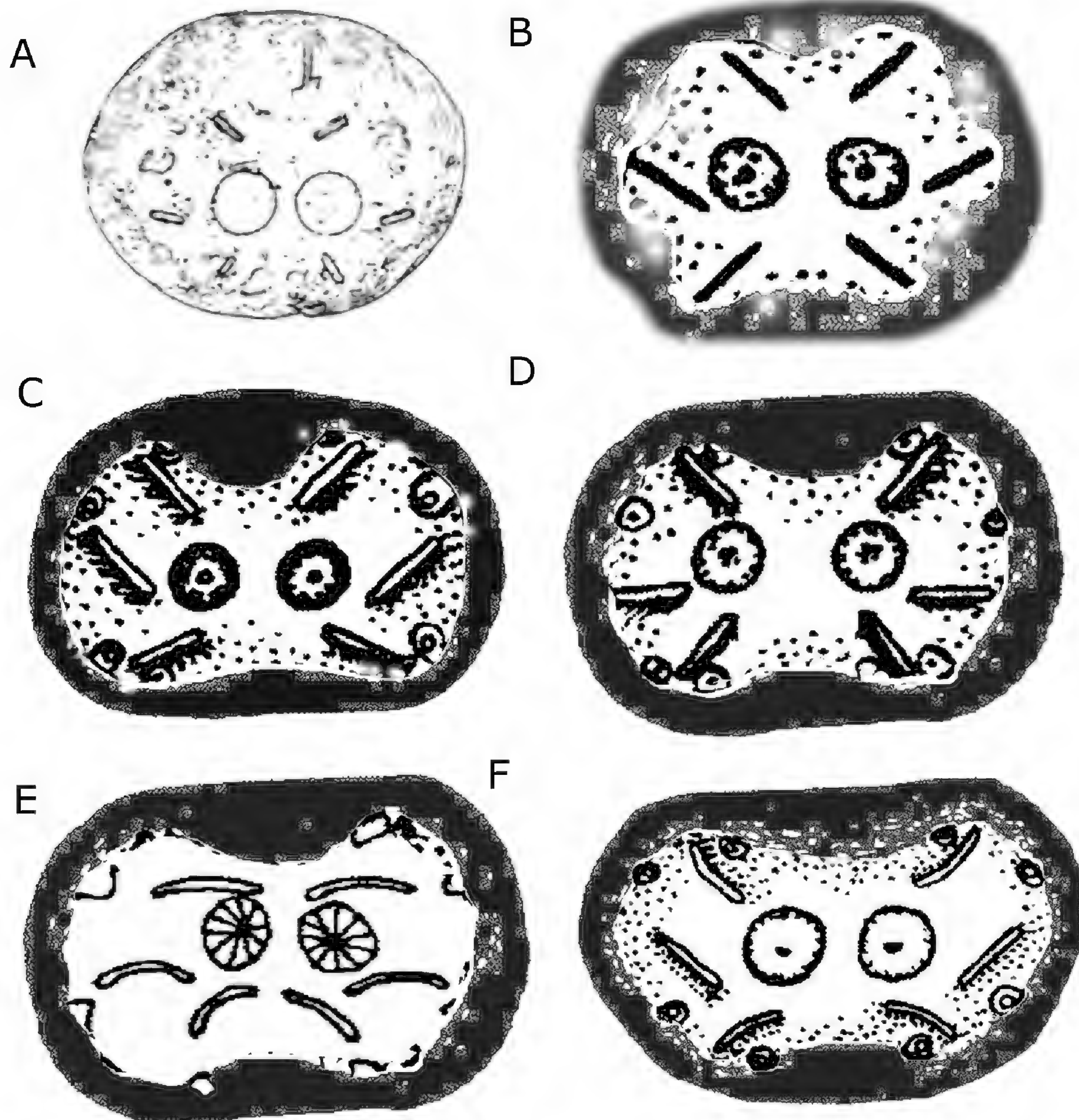


Fig. 7. Posterior respiratory process, A after Kassebeer 2000c, B–D, F after Krivosheina 2005, E after Rotheray 1996. A. *Brachyopa atlantea*. B. *Brachyopa bicolor*. C. *Brachyopa dorsata*. D. *Brachyopa pilosa*. E. *Brachyopa scutellaris*. F. *Brachyopa vittata*.

Key to the known larvae of the European species of *Brachyopa*

Note: larvae of *Brachyopa obscura*, *B. testacea*, *B. zhelochovtsevi*, *B. plena*, *B. bimaculosa*, *B. cinerea*, *B. grunewaldensis*, *B. maculipennis*, *B. quadrimaculosa*, *B. silviae*, *B. vernalis* and *B. tristis* are not known.

- 1 Body with dense spinae; posterior end of abdomen oval, usually darker than rest of the body 2
- Body at most with scattered spinae; posterior end of abdomen conical, same colour as rest of the abdomen 4
- 2 Lateral papillae on posterior segments small, tuberculate; posterior segments with several

tubercles, without rows of spinae
 *Brachyopa vittata* Zetterstedt

- At least 3 or 4 lateral papillae on posterior segments well developed, large; posterior segments with several tubercles, with clear rows of spinae 3
- 3 Lateral papillae on posterior segment unequally sized, 5th and 6th as long as wide, 7th about 1.5 times longer than wide; 3rd and 4th pair of papillae short, with short lateral appendages and 2 longer apical appendages *Brachyopa panzeri* Goffe
- Lateral papillae 5–7 on posterior segments equally sized, about 1.5 times longer than wide; all papillae with long curved appendages, some longer than papilla *Brachyopa dorsata* Zetterstedt

- 4 Abdomen without transverse rows of setae, some isolated stump like setae may be present; body coated in dark coloured blotches of various sizes .. 5
- Abdomen with rows of setae; body with blotches inconspicuous and pale, or entirely absent..... 6
- 5 A large tubercle present between the first pair of sensilla on tergum VII; setae of last three pairs of anal lappets directed apically *B. minima* Vujić & Pérez-Bañón
- Area between the first pair of sensilla flat; setae of last three pairs of anal lappets directed laterally and apically *B. insensilis* Collin
- 6 Rows of setae on abdomen strictly aligned; abdominal segments 1–6 with sensilla pairs 1 and 2 with 2 large and 2 small setae 7
- Rows of setae on abdomen not aligned; sensilla pairs 1 and 2 usually with more than 2 large setae 8
- 7 Spiracular opening on prp long and obliquely placed (Fig. 7B) *B. bicolor* (Fallén)
- Spiracular openings on prp short and medial pairs almost horizontally placed (Fig. 3A) *B. atlantea* Kassebeer
- 8 PRP > 1 mm long, as long as or longer than width of body; ventral surface of prp apically smooth, without pits *B. pilosa* Collin
- PRP < 1 mm long, shorter than width of body; ventral surface of prp apically with pits *B. scutellaris* Robineau-Desvoidy

The European species of the genus *Brachyopa* Meigen, 1822

Brachyopa atlantea Kassebeer, 2000

Brachyopa atlantea Kassebeer, 2000c: 142; ♂ and ♀ types in private collection of C.F. Kassebeer (present condition or whereabouts unknown), not studied. Figs 3A, 7A, 10A, 18A, 21A, 22

Distribution. Described from Morocco, based on five adult specimens and several puparia and larvae collected in Morocco. Only one European record from Spain (Van Steenis & Van Steenis 2014) is known. It is classified as an Ibero-Maghreb endemic species.

Biology. Adults, puparia and larvae have been found on external sap runs on *Populus* spp. in the Atlas Mountains. The species was collected at the same locality two years in a row (Kassebeer 2000c). The record from Europe was most likely from the South-Western part of the Sierra Nevada in an area with Mediterranean evergreen Oak (*Quercus ilex* Lour. and *Q. pyrenaica* Willd.) forest.

The flight period is not well known as only one adult was collected, on the 24th of March, in the field. All other records are from larvae and puparia, many of which were empty, between March 6th and April 16th (Kassebeer 2000c). The European specimen was collected on the 13th of April (Van Steenis & Van Steenis 2014).

The species has been collected at altitudes of 550 and 1000 m a.s.l.

Population fluctuations. In Morocco the species was collected at the same locality two years in a row. It is not known if the species disappeared after that or that the locality has not been visited after these years. Based on the larval habitat, external sap-runs, which tend to dry out in the course of several years (Pérez-Bañón et al. 2016) it is likely the population shows large fluctuations.

Remarks. The identification of the European specimen is based on the characters given in Kassebeer (2000b). The female specimen is listed in the database and, in the distribution map, the African distribution of this species is not shown.

Red List. Not present on any Red List. Due to its presumed relict occurrence in Europe and the small area of occupancy in Morocco this species has little flexibility of coping with threats. If major habitat threats are present, its future survival will be under severe pressure, however, the presumed forest type G2.1 is listed as “Least Concern” in the European Red List of habitats (European Commission 2016).

Brachyopa bicolor (Fallén, 1817)

Rhingia bicolor Fallén, 1817: 33; ♂ lectotype and ♀ paralectotype, in NHRS, not studied. Figs 3B, 5A, 7B, 10B, 14A, 18B, 21B, 23, 38A

Distribution. A widespread European species occurring from Southern Norway and Sweden to Spain and Greece and from Wales into the European part of Russia and Japan.

Biology. Its main habitat consists of different deciduous woodland and parkland forest types such as alluvial *Alnus-Quercus-Fraxinus*, thermophilous and xerophilous *Quercus-Ulmus-Fraxinus* forests (Reemer et al. 2009; Speight & Castella 2011; Ball & Morris 2014).

Larvae are known from a wide variety of trees, deciduous: *Aesculus hippocastanum* L., *Fagus sylvatica* L., *Platanus* spp., *Populus alba* L., *Pyrus* spp., *Quercus* spp. and *Ulmus* spp. as well as coniferous *Abies* spp., in accumulations of sap under bark of live trees or tree trunks and sap runs. Larvae are associated with sap runs caused by larvae of the caterpillar of *Cossus cossus* (Lepidoptera) and larvae of the beetles *Hylecoetus flabellicornis* (Schneider, 1791), *Trypodendron lineatum* (Olivier,

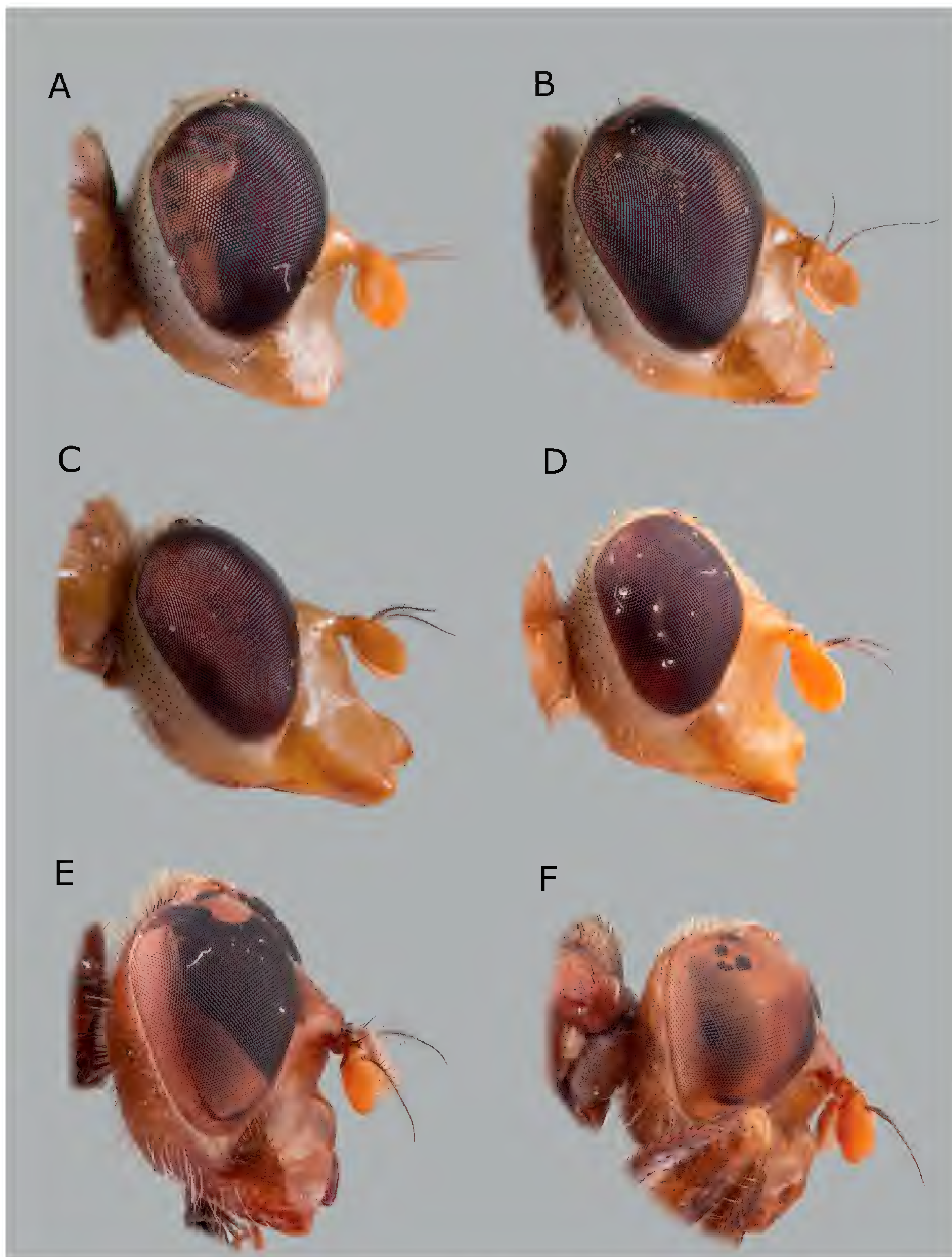


Fig. 8. Head male, lateral view. **A.** *Brachyopa obscura*, Olloy-s-Viroin Belgium. **B.** *B. testacea*, Elzetterbos, the Netherlands. **C.** *B. vittata*, Eupen, Belgium. **D.** *B. zhelochovtsevi*, Aktru, Altay, Russia. **E.** *Hammerschmidtia ferruginea*, Borjomi NP, Georgia. **F.** *H. ingraca*, Bychika, Russian Far East.

1795) and *T. signatum* (Fabricius, 1792) on *Abies* spp., *Populus tremula* L., *Quercus robur* L. and *Salix* spp. (Torp 1986; Rotheray 1991; Nielsen 2005; van Eck et al. 2016; Wolton & Luff 2016; Krivosheina 2019).

It is assumed that sap runs on *Quercus* spp. is the preferred larval habitat of this species (Ball & Morris 2014; Krivosheina 2019). One population on a single *Quercus robur* tree was monitored over a period of seven years after which the tree was storm felled. This tree had an age of 118 years and possibly over the last 20 years it suffered from drought stress and loss of hardwood creating suitable larval habitat (Wolton & Luff 2016). The larvae found in sap-runs on *Aesculus hippocastanum* and *Quercus robur* are prone to be parasitized by *Tetrastichus brachyopae* Graham, 1991 (Hymenoptera: Eulophidae), with up to 18 wasps hatching from one single puparium (Rotheray 1996; van Eck et al. 2016).

Adults were found visiting flowers of e.g. *Acer* spp., *Crataegus laevigata* (Poir.) DC., *Prunus padus* L., *P. serotina* Ehrh., *P. spinosa* L., *Valeriana* spp. (Stuke 1996; Bartsch et al. 2009; Nilsson et al. 2012), and *Platanus* spp. (database). They are more often found flying around trees such as *Acer pseudoplatanus* L., *Betula pendula* Roth, *Castanea sativa* Mill., *Populus* spp., *Salix alba* L. and the above mentioned trees with supposed sap-runs where they can fly high into the trees (Röder 1990; Torp 1994; Nilsson et al. 2007; Reemer et al. 2009; Ricarte et al. 2014; van Steenis et al. 2019; Mielczarek et al. 2019) as well as *Carpinus betulus* L., *Fagus* spp. and *Tilia* spp. (database). The larvae overwinter, with puparial formation occurring from February to May; the duration of the puparial phase is 3.5 weeks (Dussaix 2013).

The overall flight period is from the beginning of April until the end of July with extreme dates of the 6th of March and the 15th of August (Fig. 38A). There is a range shift and shortening in flight period from south to north, so that the flight period in the boreal countries is from the end of April until the end of June. Collected at altitudes of 0–1620 m a.s.l. (Maibach et al. 1992; database). This species has many records from the 19th century in several countries, e.g., Austria, Germany and Sweden, but has only rather recently been found in the Netherlands and Norway, with the first records from 1966 and 1980 respectively. The number of observations in different time periods of 50 years differs greatly between and also within countries. Over the periods before 1900, from 1900 to 1950, from 1950 to 2000 and after 2000, in Austria there were respectively 6, 2, 0 and 6 records; in Serbia 0, 0, 6 and 7 records are known, while in Sweden 2, 2, 5 and 31 records are known.

Population fluctuations. This species is associated with external sap runs on *Quercus* spp. and several other trees, and as this type of microhabitat is known to fluctuate over time this species would be expected to be adapted to such fluctuations. In light of this, it is most likely this

species shows large fluctuations, especially within marginal habitats and possibly even within large areas with suitable habitat. This conclusion can also be drawn from the fluctuating number of records as given above.

Remarks. Several of the old records of this species could actually belong to different species.

Red List. This species occurs on several regional Red Lists and is categorized from “Least Concern” to “Endangered” (Bygebjerg 2004; Farkač et al. 2005; Ssymank et al. 2011; Ball & Morris 2014; Henriksen & Hilmo 2015; Artdatabanken 2019). Even within Germany large differences between the “Bundesländer” exist where it is classified from “Data Deficient” and “Vulnerable” to “Endangered” (Pellmann et al. 1996; Stuke et al. 1998; Doczkal et al. 2001; Dziock et al. 2001; von der Dunk et al. 2003; Dziock et al. 2004). These differences depend on several factors, such as being at the edge of its distributional range and thus being at a higher threat level, the availability of new records lowering the threat category and possibly also the use of different criteria.

Brachyopa bimaculosa Doczkal & Dziock, 2004

Brachyopa bimaculosa Doczkal & Dziock, 2004: 45;
♀ holotype in SMNM, not studied
Figs 3C, 10C, 14B, 18C, 21C, 24

Distribution. Single records are known from three localities around the Alps (Germany and Slovenia) and one in central Greece. A large population has been found on the Peloponnesos, Greece (van Steenis & van Steenis 2014). This species is regarded as a European endemic.

Biology. The species is recorded in sub-alpine forests dominated by *Abies alba* Mill. and *Fagus sylvatica* along small rivers in the shade of trees such as *Acer* spp., *Alnus* spp. and *Salix* spp. (Doczkal & Dziock 2004; van Steenis et al. 2013) and on open flower-rich limestone meadows within forests dominated by *Abies cephalonica* Loudon and *Pinus nigra* J.F. Arnold. No larval records are known and adults have only been found while visiting flowers of several different plant species such as *Acer* spp., *Aegopodium podagraria* L., *Bupleurum* cf. *rotundifolium*, *Prunus* spp. and *Salix aurita* L. (Doczkal & Dziock 2004; van Steenis et al. 2013; van Steenis & van Steenis 2014).

In the Alpine population the specimens were collected on the 3rd and 19th of June at altitudes of 970 and 1050 m a.s.l. respectively (Van Steenis & Van Steenis, 2014). In the Northern part of the Schwarzwald one specimen was collected on the 31st of March between 260 and 310 m a.s.l. (Doczkal & Dziock, 2004). In Greece the species was collected between 22nd of April and the 28th of May and had an altitudinal range of 980–1700 m a.s.l. (Van Steenis & Van Steenis, 2014, database). The first record

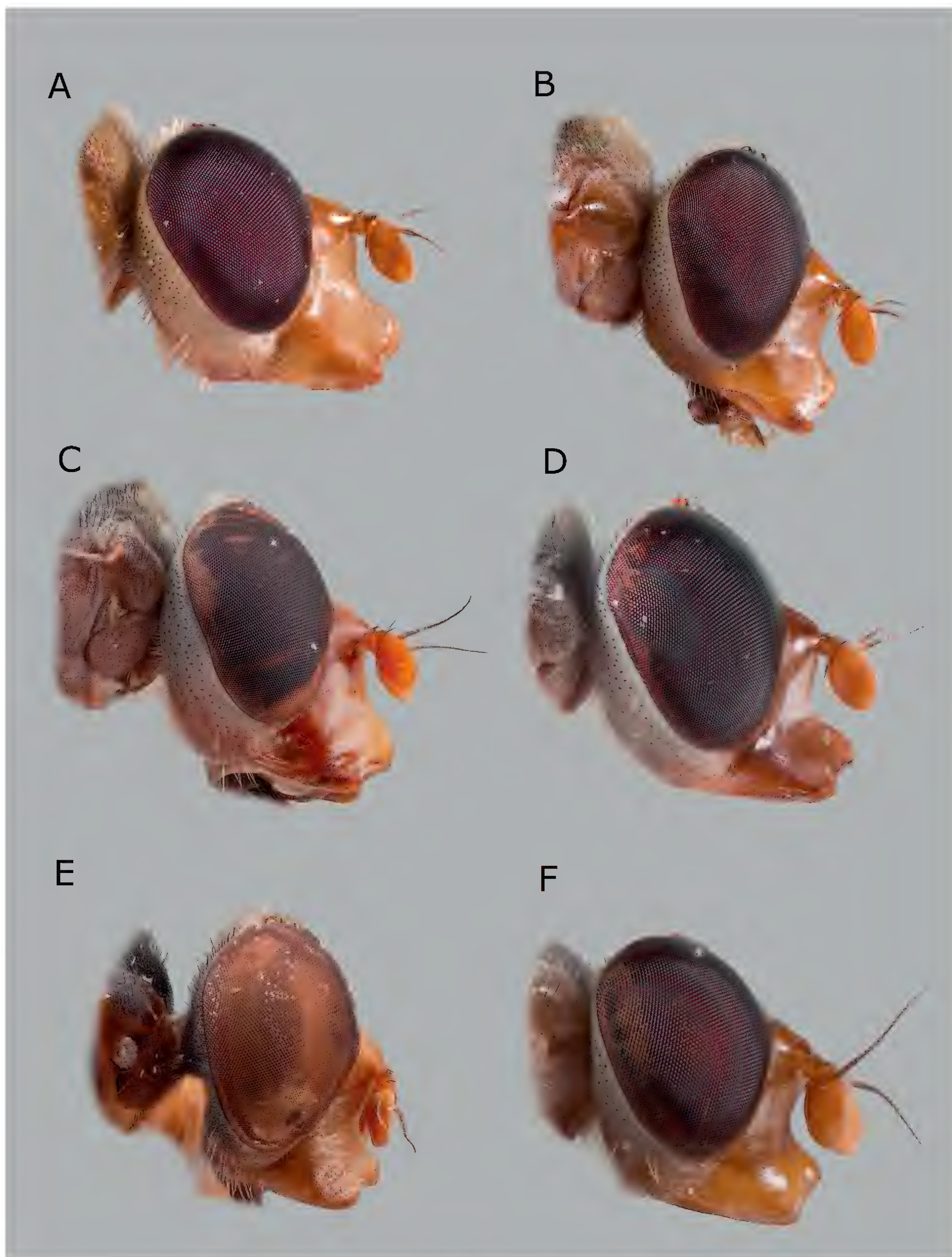


Fig. 9. Head male, lateral view. **A.** *Brachyopa dorsata*, Rocherath, Belgium. **B.** *B. panzeri*, Oudergem, Belgium. **C.** *B. maculipennis*, Fruška Gora, Serbia. **D.** *B. pilosa*, Drentsche Aa, the Netherlands. **E.** *B. plena*, Ioannina, Greece. **F.** *B. scutellaris*, Oudergem, Belgium.

dates back to 1990 and it has been seen regularly in the 21st century.

Population fluctuations. Only post 1990 records are available from very widely separated localities. It is possible this species has been recorded before 1990 but was not separated from similar species such as *B. insensilis*. No evidence was found that this species has an extreme fluctuation in populations or in population size.

Remarks. This species has a restricted range of occurrence and is only found in larger numbers on the Peloponnesos. The localities around the Alps are possibly relict populations and may not be viable for maintaining a steady population. The species distribution is severely fragmented and the seemingly large population on the Peloponnesos is not likely to colonize the Alpine localities. The larval habitats of the species of *Brachyopa* are all connected with sap-runs or accumulations of sap under bark and thus depending on natural forests with over-mature trees. This habitat is under pressure in Greece and especially on the Peloponnesos and on many Mediterranean islands due to overgrazing and forest fires (WWF 2007; Caballero 2009; Kizos et al. 2013; Kalabokidis et al. 2013).

The male specimens from the Alps differ in several morphological characters from those collected on the Peloponnesos in such a way that two species could be involved. The male genitalia as well as molecular data do not show large variation between these two putative species and further study is needed to sort out the taxonomy of the species.

Red List. This species only occurs on one regional Red List. In Germany it is regarded as “Data Deficient” as only one record was known (Ssymank et al. 2011). The habitat where the species was found in the Alpine region could be classified as G4 and possibly G4.1 both of which are categorized as “Least Concern” (European Commission 2016); the Peloponnesian Black pine forests (G3.5) are “Least Concern” too (European Commission 2016). On Mt Taygetos, where part of the population was found, the negative effect of forest fires clearly pose a great threat to this type of forest (Sarris et al. 2014) despite its classification, and thus to this *Brachyopa* species.

In the light of the possible split of this species, it is advised to treat the Alpine populations separately from the Greek populations.

***Brachyopa cinerea* Wahlberg, 1844**

Brachyopa cinerea Wahlberg, 1844: 65; types in NHRS, not studied.

Figs 3D, 10D, 14C, 18D, 21D, 24

Distribution. Found in the boreal parts of Norway, Sweden and Finland, and eastwards into the boreal zone of Siberia and Japan.

Biology. A relatively early flying subarctic species found in *Betula-Salix-Alnus* and mountain *Betula* forests visiting flowers of *Ribes rubrum* L. and *Salix glauca* L. (Nielsen 1992, 1998; Mutin 1998; Bartsch et al. 2009) and *Anthriscus sylvestris* L. (database). In the Russian Far East it is more widespread and ‘with more specimens found together visiting *Prunus padus* and *Salix bebbiana* Sarg. (Mutin et al. 2016). No larval records are known.

The flight period of this species is from the beginning of May until the middle of July (database). Collected at altitudes between 25 and 1475 m a.s.l. (database). The number of records from the 21st century equals that of the period 1950-2000. The relatively many records from the period from 1900-1950 indicate a possible decline in populations.

Population fluctuations. This species has not been collected at the same locality in different years and as only single records are known from Europe it cannot be concluded that this species shows extreme fluctuations.

Remarks. A rare and very local species, which almost always occurs as single specimens at collecting sites. Very little is known about its biology. Due to the low numbers found in Europe, it could be argued that the species is at its western limit of occurrence, and hence vulnerable to habitat changes.

Red List. This species occurs on the Red List of Finland, Norway and Sweden, and it is classified from “Near Threatened” to “Vulnerable” (Henriksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019). These categories seem to be based on weak assessments since, given its distribution, there is likely to be considerable undersampling of this species. More research is required in order to make a well founded decision on its status in Europe. The main habitat for this species, forest type G1.5, is classified as “Vulnerable” (European Commission 2016).

***Brachyopa dorsata* Zetterstedt, 1837**

Brachyopa dorsata Zetterstedt, 1837: 35; types in ZIL, not studied

Brachyopa sibirica Virolvitsh, 1982: 58, type in ZISP, (syn by Mutin & Barkalov 1991), not studied.

Figs 2A, 7C, 9A, 13A, 17A, 20A, 25, 38B

Distribution. A widespread temperate and boreal (Finland, Norway and Sweden) species with its western distributional boundary from the western part of the French Pyrenees along the Alps and the Vosges into the eastern parts of Belgium and the Netherlands, eastwards through

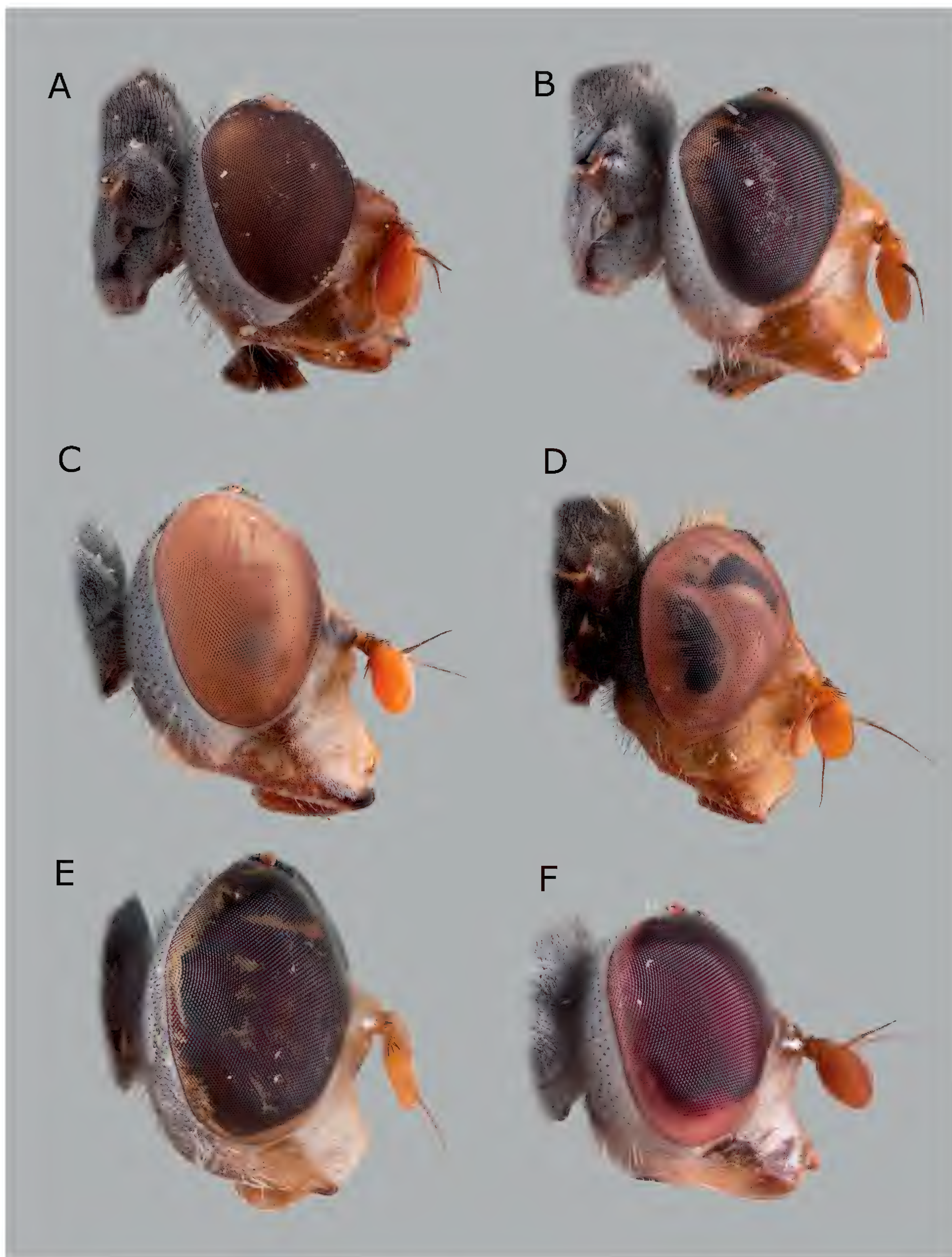


Fig. 10. Head, lateral view. **A.** *Brachyopa atlantea*, female, Granada, Spain. **B.** *B. bicolor*, male, Engsbergen, Belgium. **C.** *B. bi-maculosa*, male, Arkadia, Greece. **D.** *B. cinerea*, male, Komsomolsk-na-Amur, Russian Far East. **E.** *B. grunewaldensis*, male, Zagreb, Croatia. **F.** *B. insensilis*, male, Engsbergen, Belgium.

Serbia and European Russia into the Russian Far East and Japan. No records are known from the Mediterranean area.

Biology. The adult habitat consists of lowland to subalpine mixed forest and of palsa- (see Zuidhoff & Kolstrup 2005; van Steenis & Zuidhoff 2013) and *Pinus-Betula*-bogs in Northern Scandinavia (Hippa et al. 1981; Nielsen 1992; Reemer et al. 2007; Bartsch et al. 2009).

Larvae are found in accumulations of sap under bark of trunks and stumps of *Betula* spp., *Populus tremula* and *Ulmus* spp. often together with other Diptera larvae: *Libnotes ladogensis* (Lackschewitz, 1940) and *Gnophomyia acheron* Alexander, 1950 (both Limoniidae), *Hammer-schmidtia ingriscia* Stackelberg, 1952 (Syrphidae), *Solva semota* Krivosheina, 1972 (Xylomyidae) and larvae of the beetle *Hylecoetus dermestoides* (Linnaeus, 1760) (Lymexylidae) (Mutin 1998; Krivosheina 2005, 2019).

Found on flowers of *Acer platanoides* L., *Caltha palustris* L., *Crataegus* spp., *Euphorbia cyparissias* L., *Malus sylvestris* (L.) Mill., *Prunus domestica* ssp. *insititia*, (L.) Bonnier & Layens, *P. padus*, *Rubus chamaemorus* L., *Salix* spp. (Hippa et al. 1981; Nilsson et al. 2007; Reemer et al. 2007; Bartsch et al. 2009; van Steenis 2011; Nilsson et al. 2012; Speight 2020), and also *Anthriscus sylvestris* (L.) Hoffm., *Geranium sylvaticum* L., *Prunus avium* (L.) L., *Salix udensis* Trautv. & C.A. Mey. and *Spirea* spp. (database). Adults are more often found near trunks and stumps of *Betula* spp. and damaged coniferous trees or at sap runs on *Fagus* spp. and *Quercus* spp. (Röder 1990; Mutin et al. 2016; Mielczarek et al. 2019). In the Russian Far East, it is found near damaged coniferous trees together with several other *Brachyopa* species such as *B. panzeri*, *B. testacea* and *B. zhelochovtsevi* (Mutin et al. 2016). Larvae are found in tunnels created by Lymexylidae larvae from *Betula* and *Ulmus* (Krivosheina, 2005) and under bark of *Fagus*, *Picea*, *Populus* and *Quercus* trees (Mutin 1998; Dussaix, 2020).

This species has a main flight period (Fig. 38B) from the beginning of April until the end of July, with extreme dates of the 17th of March and the 5th of August. The altitude at which this species is collected range from 0–1503 m a.s.l. (database). It has been found in fluctuating numbers during different periods in Austria and Germany, with relatively many records from before 1900. In several other countries it has been recorded increasingly many times since 1980 (Sweden), 2007 (Netherlands) and 2009 (Belgium) indicating a possible extension of its distributional range.

Population fluctuations. No clear trends are published, but based on the larval habitat it seems likely this species will not exhibit strong population fluctuations. The larval habitat consists of trunks and stumps of a wide variety of tree species which form a natural and rather constant factor in European forests.

Remarks. This is a species that has been misidentified in many instances. References before 1980 should be treated with special care (cf. Reemer et al. 2007). The discriminating characters were first fully understood by Thompson (1980), but even since then, this species and *Brachyopa panzeri* have been mixed up (e.g. Stuke et al. 2000; Mielczarek et al. 2019). It seems that *B. dorsata* is the more northern and Alpine species, and has recently spread to the Netherlands and Belgium (Bot & Van de Meutter 2019).

Red List. This species is mentioned in four regional Red Lists and was either not evaluated or assumed to be of “Least Concern” (Bygebjerg 2004; Ssymank et al. 2011; Henriksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019).

Brachyopa grunewaldensis Kassebeer 2000

Brachyopa grunewaldensis Kassebeer 2000a: 8; ♂ holotype in private collection of C.F. Kassebeer (present condition or whereabouts unknown), not studied. Figs 3E, 10E, 14D, 21E, 26

Distribution. A temperate and southern European species with a very scattered distribution from Spain in the west, to Belgium and the eastern part of Germany in the north, and to Slovakia in the east. Also known from several countries on the Balkan Peninsula. This species is regarded as a European endemic.

Biology. Adults are found in Mediterranean acidophilus *Quercus-Fraxinus* forests, mixed thermophilus *Quercus-Carpinus* and *Fagus-Picea* forests, alluvial *Quercus-Populus* and *Carpinus* forest and riparian *Platanus* forest (Kassebeer 2000a; Doczkal & Dziöck 2004; van Steenis et al. 2019; Speight 2020).

The larva is unknown but adults were collected in emergence traps on *Fraxinus angustifolia* Vahl, *Quercus faginea* Lam. and *Q. pyrenaica*, indicating the larvae live in rot-holes in at least these tree species (Ricarte et al. 2013).

It visits flowers of *Acer* spp., *Crataegus monogyna* Jacq., *Pyrus spinosa* Forssk., *Sorbus torminalis* (L.) Crantz and *Tamarix* spp. (Marcos-García 1987; van Steenis & van Steenis 2014; Mielczarek et al. 2019; Speight 2020) and flies close to trees with sap runs including *Aesculus hippocastanum*, *Carpinus betulus*, *Castanea sativa*, and *Quercus* spp. (Doczkal & Dziöck 2004; Mielczarek et al. 2019; van Steenis et al. 2019; Speight 2020), and *Acer* spp. (database).

This widely distributed but very scattered species has been collected between the 8th of April and the 16th of June, with extreme dates of the 28th of February and the 16th of July. There are no indications of differences between southern and northern populations (Kassebeer

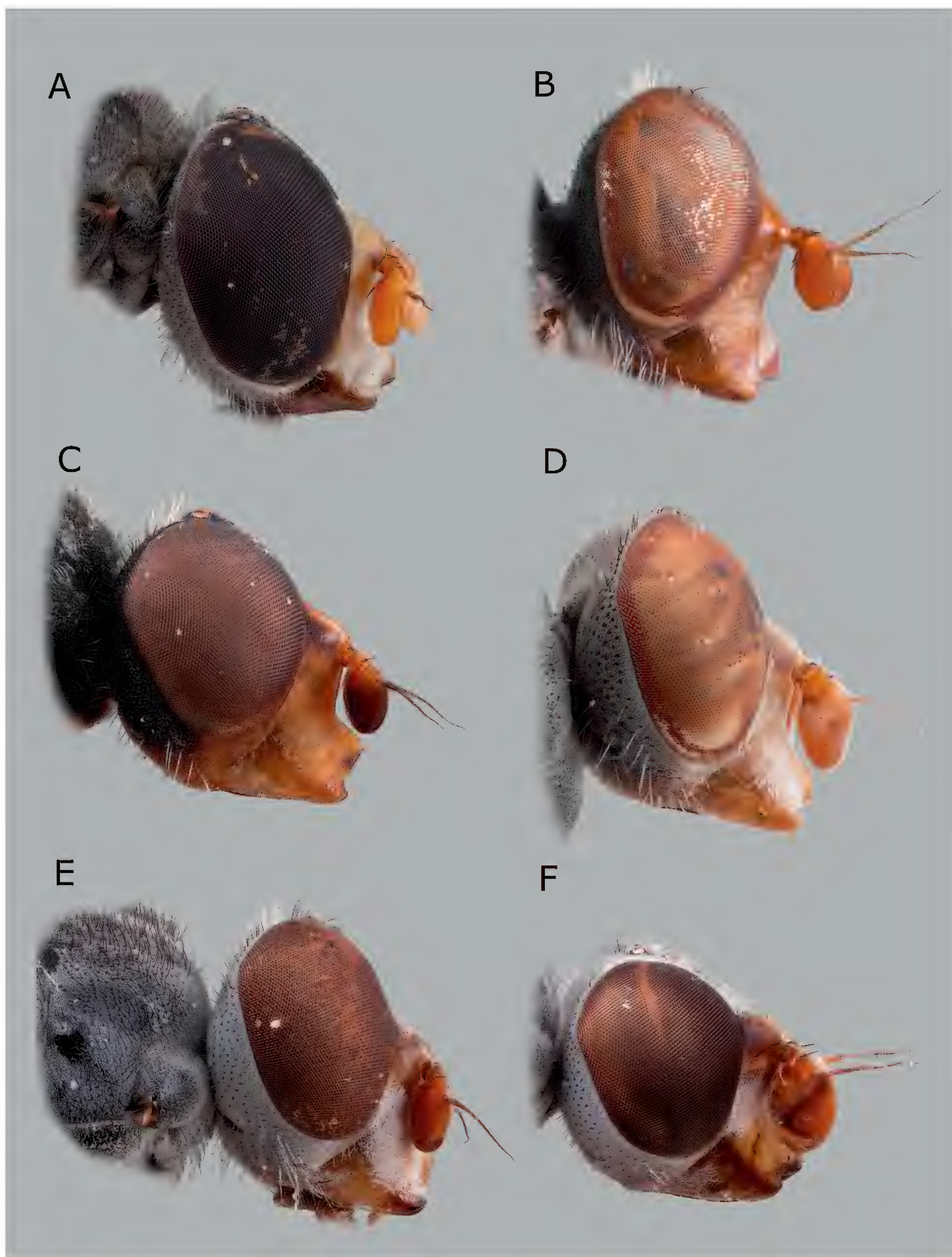


Fig. 11. Head, lateral view. **A.** *Brachyopa cruriscutum*, male paratype, Hakkari, Turkey. **B.** *B. silviae*, male, Bringhausen, Germany. **C.** *B. minima*, male, Lesvos, Greece. **D.** *B. vernalis*, male paratype, Crete, Greece. **E.** *B. quadrimaculosa*, male, Samos, Greece. **F.** *B. quadrimaculosa*, female, Samos, Greece.

2000; Doczkal & Dziöck 2004, database). Collected at altitudes of 50–1700 m a.s.l. (database). The first record dates from 1969, and most of its records are from the 21st century. This is most likely due to the fact that more entomologists know this species and thus tend to collect it more often.

Population fluctuations. This species is only recently described and it seems to be a very rare but widespread species. The habitat preferences are not fully known and, as such, it is impossible to know whether this species might undergo population fluctuations.

Remarks. This is a recently described species confused with *B. bicolor* in the past and possibly more widespread than presently known. The habitat preferences are not well known and it might be a very specialized species with high demands on its habitat. This will make the species more vulnerable to habitat changes and thus its future survival more threatened.

Red List. It is only listed on the German Red List under category “Endangered” (Ssymank et al. 2011). The habitat of this species consists of a wide range of different forest types and each of these types is classified in a different threat category. The Mediterranean acidophilus forest (G1.8) is “Vulnerable” while the thermophilous forests (G1.7 and G4.6) are classified as “Least Concern”. The alluvial forests (G1.1–G1.3) are categorized from “Near Threatened” to “Endangered” (European Commission 2016). The precise habitat preferences are not well known and due to its very scattered distribution and low population density nothing can be concluded about its main habitat. The combination of low population density, the very scattered occurrence and the supposed threat to several of its habitats indicates that this species is at risk. The database does not provide any evidence to estimate any overall population trend or possibility of fluctuating populations and so the exact threat category is unknown as this can only be estimated by applying the IUCN Red List criteria.

Brachyopa insensilis Collin, 1939

Brachyopa insensilis Collin, 1939: 105; ♂ lectotype, 4 ♂♂, 3 ♀♀ paralectotypes in UMO, studied. Figs 3F, 5B, 10F, 14E, 18E, 21F, 27, 38C

Distribution. A widespread European species from southern Sweden south to Spain, Italy and Greece and from Ireland through central Europe into the European part of Russia. It is regarded as European endemic species.

Biology. Found in a wide variety of wooded habitats from tree-lined streets in cities to broadleaved and mixed forests and often found flying around sap runs on trees

in these situations (e.g., Torp 1994; Bartsch et al. 2009; Reemer et al. 2009).

Larvae are found in a wide variety of external sap runs on broadleaved trees: *Acer pseudoplatanus*, *Aesculus hippocastanum*, *Alnus glutinosa* (L.) Gaertn., *Betula* spp., *Cornus mas* L., *Fagus* spp., *Populus* spp., *Quercus* spp. and *Ulmus glabra* Huds. and also on coniferous trees: *Abies alba* and *Pinus nigra* (e.g. Trop 1979; Claussen 1985, Rotheray 1991, 1996; Schmid & Grossmann 1996; Stubbs & Falk 1996; Bygebjerg 2001; van Steenis et al. 2001; Dussaix 2013; Ricarte et al. 2014; van Steenis & van Steenis 2014; Krivosheina 2019).

The larvae are found together with larvae of the wood gnat *Mycetobia pallipes* Meigen, 1818 (Diptera: Anisopodidae) (Krivosheina 2019). Large and small larvae are present in the sap runs at the same time as the flight period of the adults indicating a life cycle of more than one year for the larvae (Rotheray 1996). Larvae, found on *Quercus robur*, were infested by *Tetrastichus brachyopae* (Hymenoptera: Eulophidae) (van Eck et al. 2016). Infestation with parasitoid wasps, possibly *T. brachyopae*, was also observed in reared larvae collected from *Pinus nigra* on the Peloponnesos, Greece (J. van Steenis, pers. obs.).

Several species of flowers are visited by adults such as *Aegopodium podagraria*, *Anthriscus sylvestris*, *Malus sylvestris*, *Photinia* spp., *Prunus padus* and *Sorbus* spp. (Torp 1973; Claussen 1985; de Buck 1990; Bygebjerg 2001; Bartsch et al. 2009; Speight 2020) and *Cornus mas*, *Prunus serotina*, *P. spinosa* and *Pyrus* spp. (database). In many instances adults were found flying around sap runs on these larval trees and also on the following trees: *Platanus* spp., *Salix alba* (Mielczarek et al. 2019; van Steenis et al. 2019), and *Acer campestre* L., *Betula* spp., *Carpinus* spp., *Fraxinus excelsior* L. and *Populus* spp. (database).

The main flight period (Fig. 38C) is from the beginning of April until the end of July with extreme dates of the 27th of March and the 30st of August. These early and late extremes were found in SE Europe only, but no clear differences in main flight period between other southern or northern populations has been found (database). Found from sea level up to 1760 m a.s.l. (database). The records of this species are not evenly distributed over different time periods in different countries. In several countries such as Denmark and Germany the species has many records from before 1920 and only few recent records. In other countries, such as Great Britain, Hungary, the Netherlands and Sweden, the first records date from around 1950 with most records from the 21st century, although in Sweden there are large gaps of three to eight years in which no records are available. The records from Austria, Belgium and France are mostly from the 21st century (database).

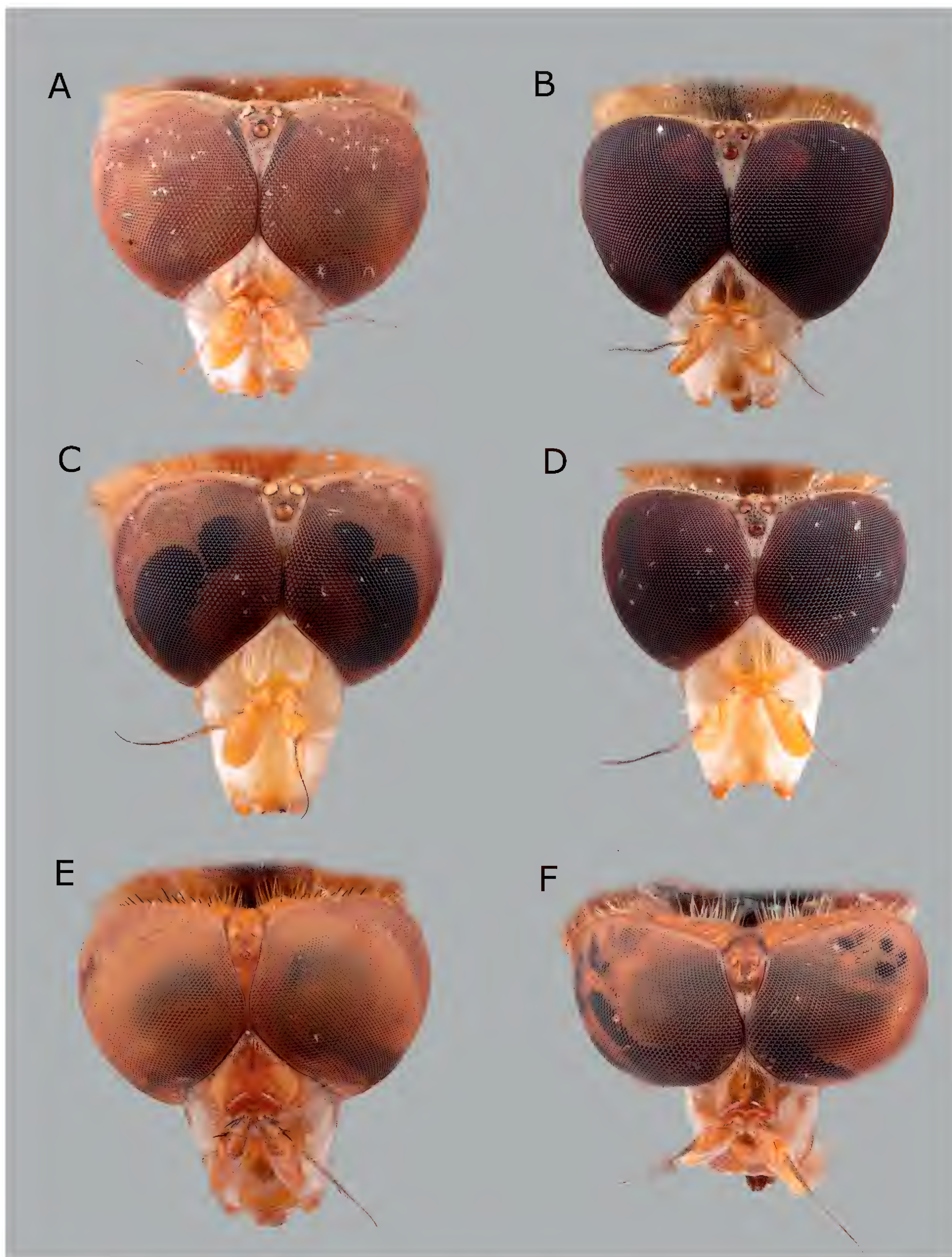


Fig. 12. Head male, dorsal view. **A.** *Brachyopa obscura*, Fiby urskog, Sweden. **B.** *B. testacea*, Elzetterbos, the Netherlands. **C.** *B. vittata*, Mångkarbo, Sweden. **D.** *B. zhelochovtsevi*, Aktru, Altay, Russia. **E.** *Hammerschmidtia ferruginea*, Riikanmaa, Finland. **F.** *H. ingrlica*, Bychika, Russian Far East.

Population fluctuations. This species is very likely to have a strongly fluctuating population size and density since it is highly dependent upon external sap runs. These sap runs tend to dry out over a short period of time causing fluctuations in suitable larval habitat (e.g., Pérez-Bañón et al. 2016). The occurrence tends to follow several tree specific diseases (see more under remarks) causing large fluctuations in the availability of larval habitat. Population fluctuations could also be argued from the fluctuating records noted above.

Remarks. Previously in Great Britain this species was believed to be dependent on sap runs on *Ulmus* spp. (Robinson 1953; Stubbs & Falk 1996). This was probably influenced by Dutch Elm disease, a vascular wilt disease affecting leaves and causing death of the tree within several years, creating many damaged trees. This first “wave” of Dutch Elm disease entered England in 1927 and died out around 1940, and was a mild one causing delayed growth and only slightly damaging trees. A more aggressive form was first noticed around 1960 and by 1990 hardly any Elm trees were left (Clouston & Stansfield 1979; Holmes & Heybrook. 1990; Harris 2017). This century the available larval habitat has increased (Sjuts 2004) again since 2001–2002 throughout Western Europe due to the bleeding canker affecting *Aesculus hippocastanum* trees (e.g. de Keijzer et al. 2012; Laue 2014; Pirc et al. 2018). This increase in larval habitat will eventually decrease again due to recent discoveries of methods to stop this disease (de Keijzer et al. 2012), and there are also indications that trees naturally become more and more resistant to this bacteria (Pánková et al. 2015) thus decreasing the number of affected trees and hence suitable larval habitat.

Molecular data show two separate groups (J.H. Skevington, pers. comm.), one from the Peloponnesos and the other from the rest of Europe indicating some kind of gene flow barrier and possible speciation.

Red List. This species occurs on several regional Red Lists and is mostly classified as “Least Concern” (Bygebjerg 2004; Ssymank et al. 2011; Ball & Morris 2014; Artdatabanken 2019) but also “Vulnerable” (Farkač et al. 2005).

Brachyopa maculipennis Thompson, 1980

Brachyopa maculipennis Thompson, 1980: 211; new name for *Musca arcuata* Panzer, 1798: 15, primary homonym preoccupied by Linnaeus (1758); type in private collection of Panzer (presumably lost), not studied.

Brachyopa arcuata var. *lateralis* Oldenberg, 1916: 105; type in DEI, (syn by Peck 1988), not studied.

Figs 2C, 9C, 14F, 20C, 28, 38D

Distribution. This is a temperate European species with scattered records from Germany in the north to Italy in the south, eastwards to Ukraine. This species is endemic to Central Europe.

Biology. The main habitat consists of alluvial *Salix-Tilia-Populus* forest and to a lesser extent also humid broad-leaved *Fagus* spp. forest with *Populus alba*, *Quercus petraea* (Matt.) Liebl. and some scattered *Pinus* spp. (Radenković et al. 2004; Mielczarek et al. 2019; van Steenis et al. 2019).

Adults have been found near external sap-runs on *Populus alba* and *Salix alba* (van Steenis et al. 2019) and on *Aesculus* spp. (database), and it is assumed that these sap-runs form the larval habitat of the species. In Poland oviposition was observed on senescent *Populus alba*. The oviposition took place about 15 cm away from the sap run (P. Trzciński, pers. comm.). Adults visit flowers of *Crataegus* spp., *Malus* spp., *Prunus padus* and *Frangula alnus* Mill. (as *Rhamnus frangula* L.) (Mielczarek et al. 2019; Speight 2020).

The species is collected between the 7th of April and 24th of June (Fig. 38D) at altitudes of 70–800 m a.s.l. The species seems to be collected relatively often in the 19th and 21st century, but with a strong decline in the first half of the 20th century. Many of the old records are from Croatia, Germany, Italy and Slovakia (database).

Population fluctuations. As with other species dependent on external sap-runs, such as *B. insensilis* and *B. minima*, it is very likely that this species also shows fluctuations in population size and densities over several decades. In Germany and Italy there are only old records and the species seems to be Critically Endangered in these countries although Germany does seem to have some post-2000 records (https://diptera.info/forum/viewthread.php?thread_id=6239) but the precise information was not available for this paper. In Serbia and especially the Czech Republic and Poland there are several recent records (Mielczarek et al. 2019; van Steenis et al. 2019) indicating there are still flourishing populations.

Remarks. The species is easy to identify and does not seem to be misidentified (e.g. Sommaggio 2007). Its occurrence is unlikely to have been overlooked in Austria, Germany or Italy in recent years, indicating that the evidence of decline is a true decline.

Red List. This species is listed as “decreasing” in the Balkan Peninsula (Vujić et al. 2001), “Endangered” in the Czech Republic (Farkač et al. 2005) and “Critically Endangered” in Germany (Ssymank et al. 2011). It is a very rare species with few and scattered records throughout its distributional range. Especially in the northern and western edge of its distribution there are mostly old records indicating a strong decline. The habitat from

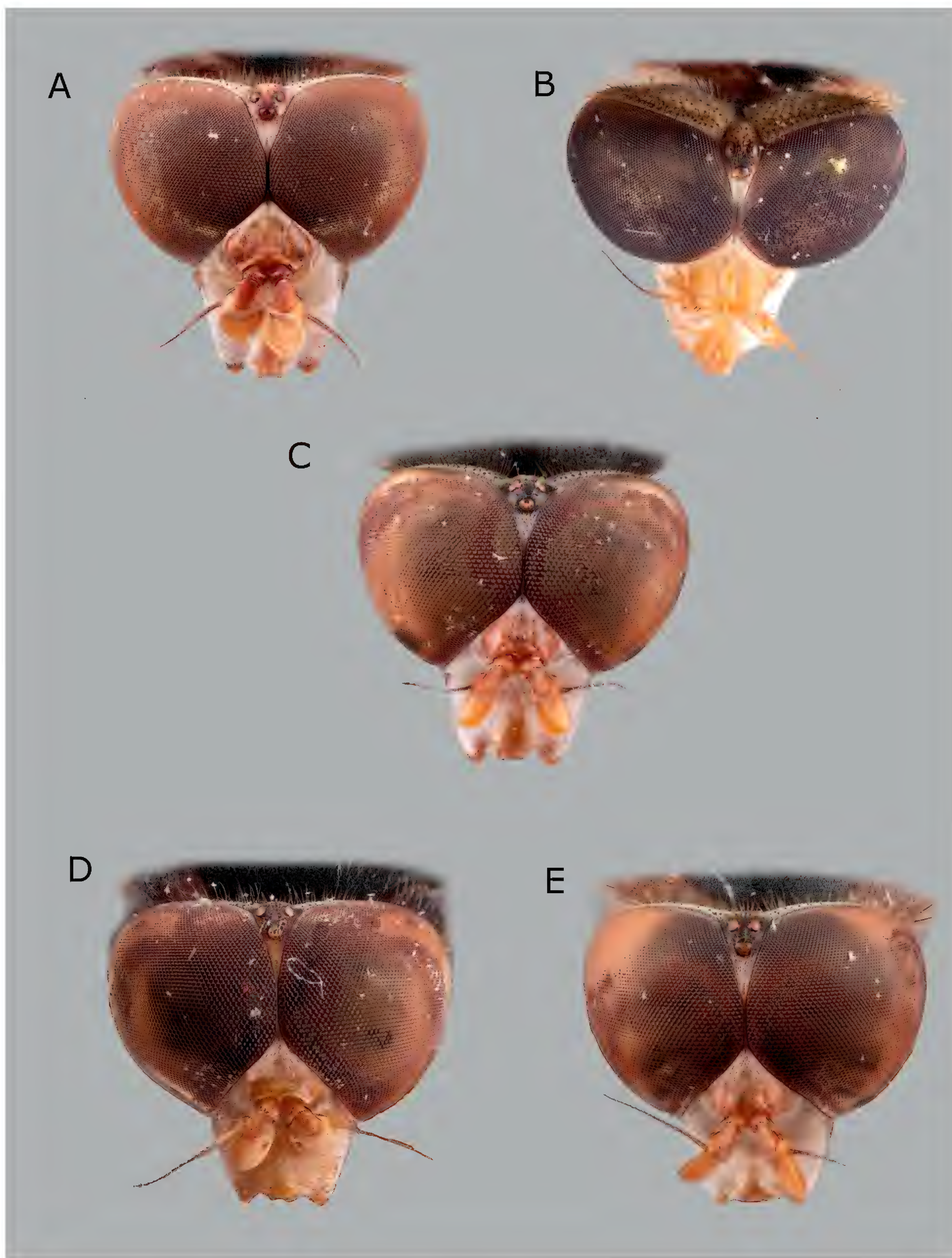


Fig. 13. Head male, dorsal view. **A.** *Brachyopa dorsata*, Den Treek, the Netherlands. **B.** *B. panzeri*, Beek (Gld), the Netherlands. **C.** *B. pilosa*, Hågadalen, Sweden. **D.** *B. plena*, male, Ioannina, Greece. **E.** *B. scutellaris*, Eure et Loire, France.

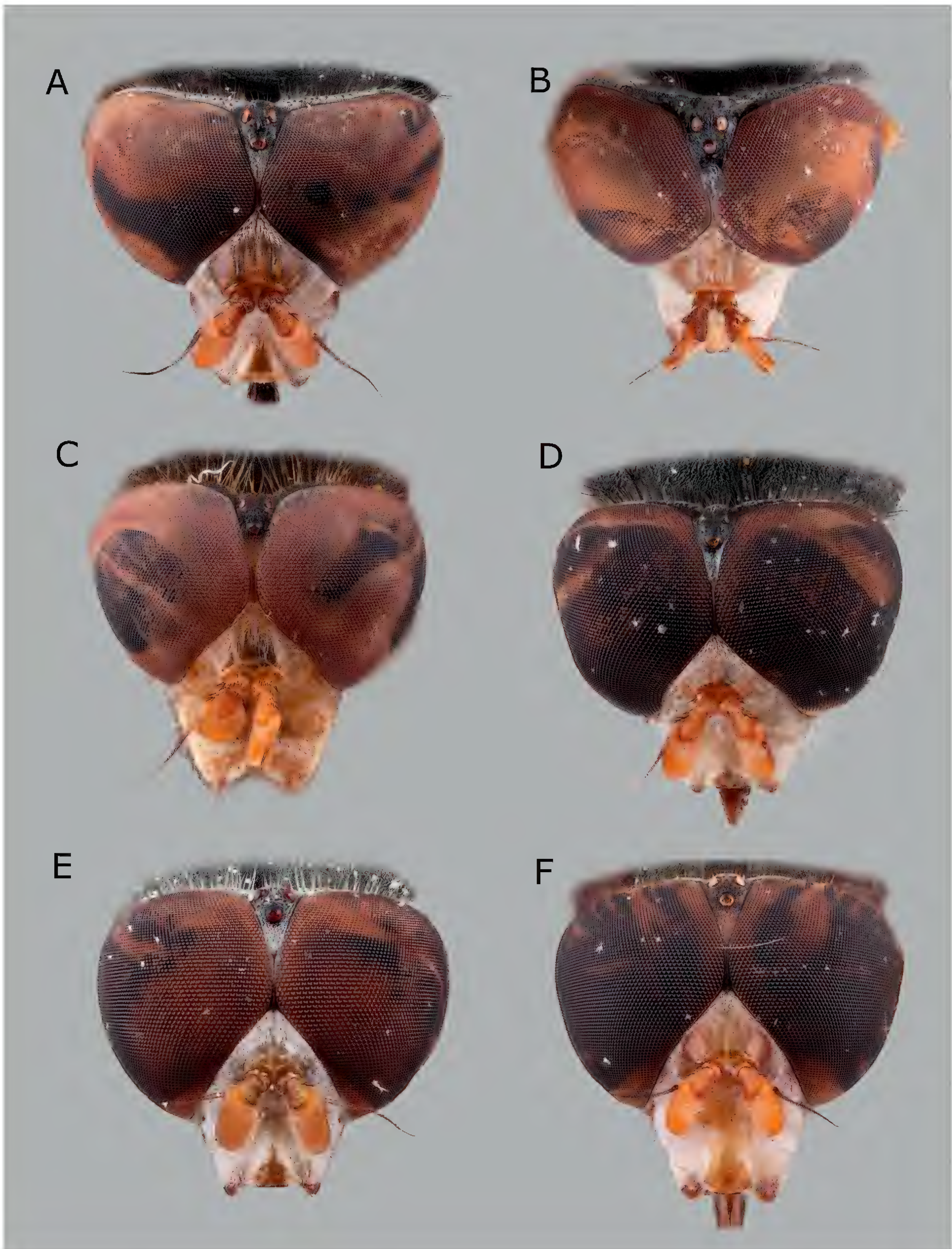


Fig. 14. Head male, dorsal view. **A.** *B. bicolor*, Novi Sad, Serbia. **B.** *B. bimaculosa*, Bolchenachtall, Germany. **C.** *B. cinerea*, Kom-somolsk-na-Amur, Russian Far East. **D.** *B. grunewaldensis*, Arkadia, Greece. **E.** *B. insensilis*, Novi Sad, Serbia. **F.** *B. maculipennis*, Fruška Gora, Serbia.

which this species is known can be categorized as riparian forests under EUNIS classification G1.1 to G1.3 and G1.A. These forest classes are considered “Vulnerable” to “Endangered” on the Red List of European habitats (European Commission 2016). The area and quality of the alluvial forests in Europe are rapidly declining (Secerov & Nevenic 2004; Hughes et al. 2012) and, as such, this habitat and *Brachyopa maculipennis* could be classified as “Endangered” or even “Critically Endangered”.

***Brachyopa minima* Vujić & Pérez-Bañón in Pérez-Bañón et al. 2016**

Brachyopa minima Vujić & Pérez-Bañón in Pérez-Bañón et al. 2016: 220; ♂ holotype, 6 ♂♂, 3 ♀♀ paratypes in FSUNS and ♀ paratype in MZH, studied. Figs 4C, 11C, 15B, 22

Distribution. Only known from two localities in Greece, on Lesbos Island from one single *Populus nigra* tree, and northern Greece (Vujić et al. 2020). It is assumed to be a European endemic.

Biology. Larvae were found from the 26th of April until the 3rd of May and on the 13th and the 28th of September. The adults and larvae were all found on a single *Populus nigra* tree with a large wound creating a slime-flux with different larval stages of several species present: *Brachyopa* aff *pilosa* and *B. quadrimaculosa*. The *B. minima* larvae survived desiccation for two years, as found in the similar *B. insensilis*. The tree was part of a small *Populus* stand along a small stream, otherwise surrounded by olive groves. The *Populus nigra* tree was the only one in a large area with a visible sap run (Pérez-Bañón et al. 2016).

Collected between the 12th of April and the 3rd of May at altitudes between 25 and 225 m a.s.l. (database).

Population fluctuations. It seems very likely this species shows extreme fluctuations in population size as it is highly dependent on naturally occurring external sap-runs on old *Populus* trees. These sap-runs are known to be scarce on the island of Lesbos and tend to heal over after relatively short periods of time (Pérez-Bañón et al. 2016), mostly no longer than 10 years.

This species seems to be at risk due to overgrazing, mainly by sheep (Kizos et al. 2013), and forest fires (Kallabokidis et al. 2013) which are major threats to the natural forests on Lesbos (Pérez-Bañón et al. 2016).

Remarks. This species belongs to a widespread species complex with possibly more undescribed Mediterranean species.

Red List. This species is not mentioned in any Red List as it has only very recently been described. Based on its

restricted occurrence and the possible threat to the habitat, as outlined above, this species is severely threatened.

***Brachyopa obscura* Thompson & Torp, 1982**

Brachyopa obscura Thompson & Torp, 1982: 441; ♂ holotype and 8 ♂♂ paratypes in ZISP, studied here. Figs 1A, 8A, 12A, 16A, 19A, 29, 39A

Distribution. A widespread northern species with a disjunct distribution in other parts of central and south-eastern Europe. Its occurrence east of European Russia is unknown but likely.

Biology. It is associated with mixed boreal forests with overmature trees such as *Betula* spp., *Populus tremula* and *P. nigra* and other rich deciduous forests of the “*Alnion glutinosae*” and “*Alno-Ulmion*” classes (Nielsen 1992; Stuke 2001b; Bartsch et al. 2009; Wakkie et al. 2011; Pétremand et al. 2020). Unlike the very similar adults of *B. testacea*, it is very rare in coniferous dominated forests.

The larva is unknown but there is one record of an adult which hatched from the bark of a *Pyrus* spp. (Nielsen 2005), indicating the larvae live in accumulations of sap under bark or in internal sap-runs.

This species has been collected on flowering herbs and bushes such as *Acer platanoides*, *Aegopodium podagraria*, *Anthriscus sylvestris*, *Crataegus* spp., *Prunus padus*, *P. serotina*, *P. spinosa*, *Ribes alpinum* L. and *Salix* spp. (van Steenis 1998; Stuke 2001b; Haarto & Kerpolla 2007; Nilsson et al. 2007; Bartsch et al. 2009; van Steenis 2011; Nilsson et al. 2012; Mielczarek et al. 2019) and *Filipendula ulmaria* (L.) Maxim (database).

The overall flight period is from May to July (Fig. 39A) and the Northern populations have a flight period from the 2nd of May to the 2nd of July, with an extreme datum of 15th of July. The other scattered records throughout east and central Europe are from the 20th of April to the 21st of June. The altitudinal range is from 40–1560 m a.s.l. (database).

Population fluctuations. Population size increased strongly a few years after a large storm during which several *Populus tremula* trees were felled (Nilsson et al. 2007, 2012). Based on these observations in Sweden this species shows an extreme fluctuating population size.

Remarks. The records in central and south-eastern Europe could be interpreted as isolated populations. The extreme fluctuations in population size, in combination with the lack of suitable habitat, could account for the fact that *B. obscura* records are so scattered over this part of Europe.

Red List. This species is reported in the Fennoscandian Red Lists as of “Least Concern” to “Endangered” (Hen-

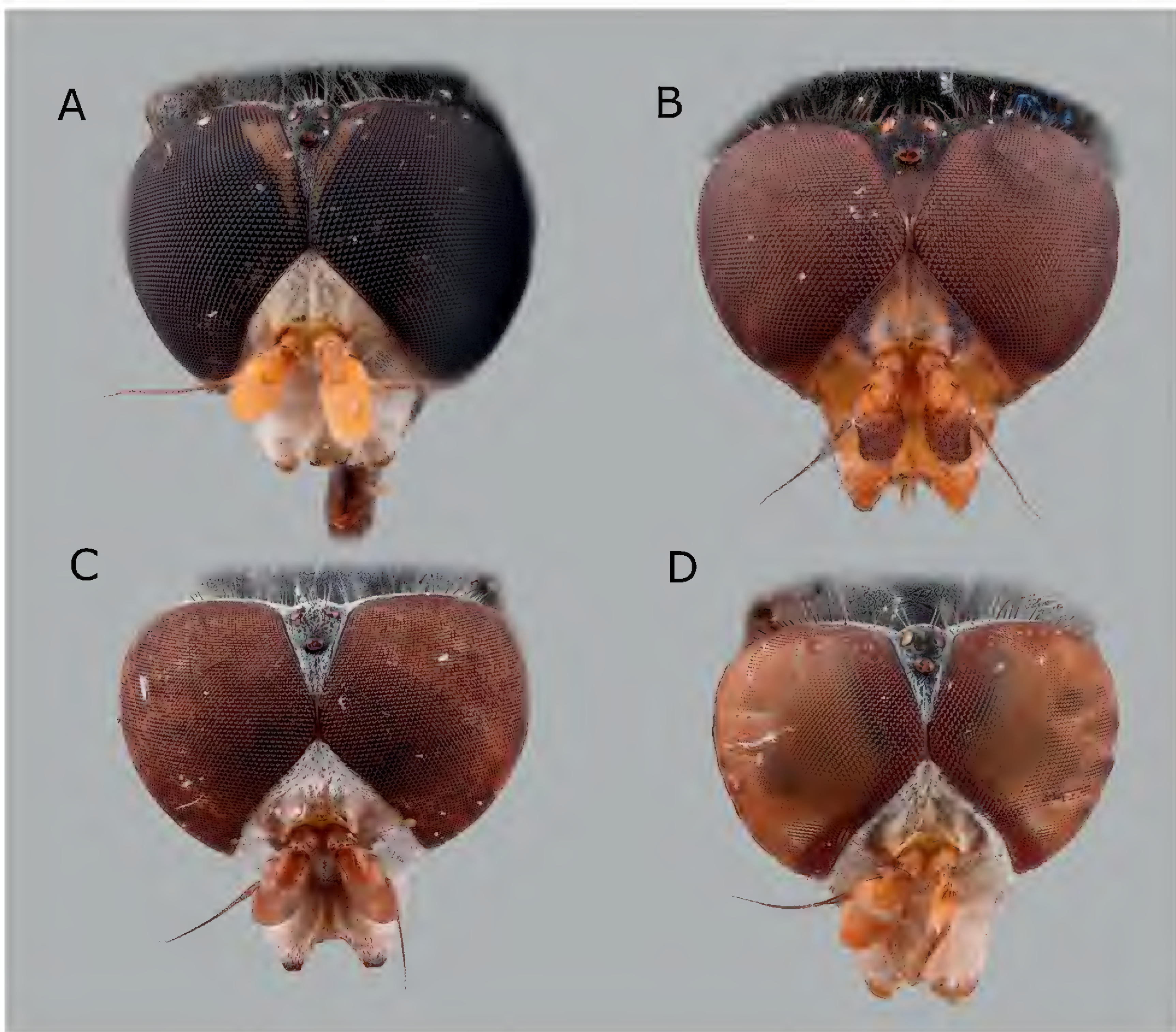


Fig. 15. Head male, dorsal view. **A.** *Brachyopa cruriscutum*, male paratype, Hakkari, Turkey. **B.** *B. minima*, male, Lesvos, Greece. **C.** *B. vernalis*, male paratype, Crete, Greece. **D.** *B. quadrimaculosa*, male, Samos, Greece.

riksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019). In Germany it is very rare and not put into any Red List category (Ssymank et al. 2011). On the Balkan Peninsula it occurs in a very small and restricted area and is categorized as “Threatened” (Vujić et al., 2001).

It has a wide occurrence in Fennoscandia and a very disjunct distribution in other parts of Europe and regional differences in threat category are to be expected.

***Brachyopa panzeri* Goffe, 1945**

Brachyopa panzeri Goffe, 1945: 278; new name for *conica* Panzer, 1798: 20, junior primary homonym, according to Thompson (1980) preoccupied by Gmelin (1790); type in private collection of Panzer or NWM (presumably lost), not studied.

Figs 2B, 9B, 13B, 17B, 20B, 30, 39B

Distribution. Widespread in northern and temperate Europe from southern Sweden to Spain and from central France eastwards through European Russia and into Siberia.

Biology. Mostly found in humid *Fagus* forests but also in alluvial *Populus* forest, mixed *Carpinus-Quercus-Pinus* forests and even in coniferous forests (Torp 1994; Lauterbach 2001, 2002; Reemer et al. 2009).

The larva has been found in a sap run on *Fagus sylvatica* (Stuke & Schulz 2001) and maybe also in a *Picea* spp. stump in the larval tunnels of *Hylecoetus flabellicornis* (Coleoptera: Lymexylidae) (Krivosheina 2005). The larvae are found together with larvae of *Gnophomyia lugubris* (Zetterstedt, 1838) (Diptera: Limoniidae), *Mycetobia pallipes* (Diptera: Anisopodidae) and with *Brachyopa vittata* (Krivosheina 2019). The records from

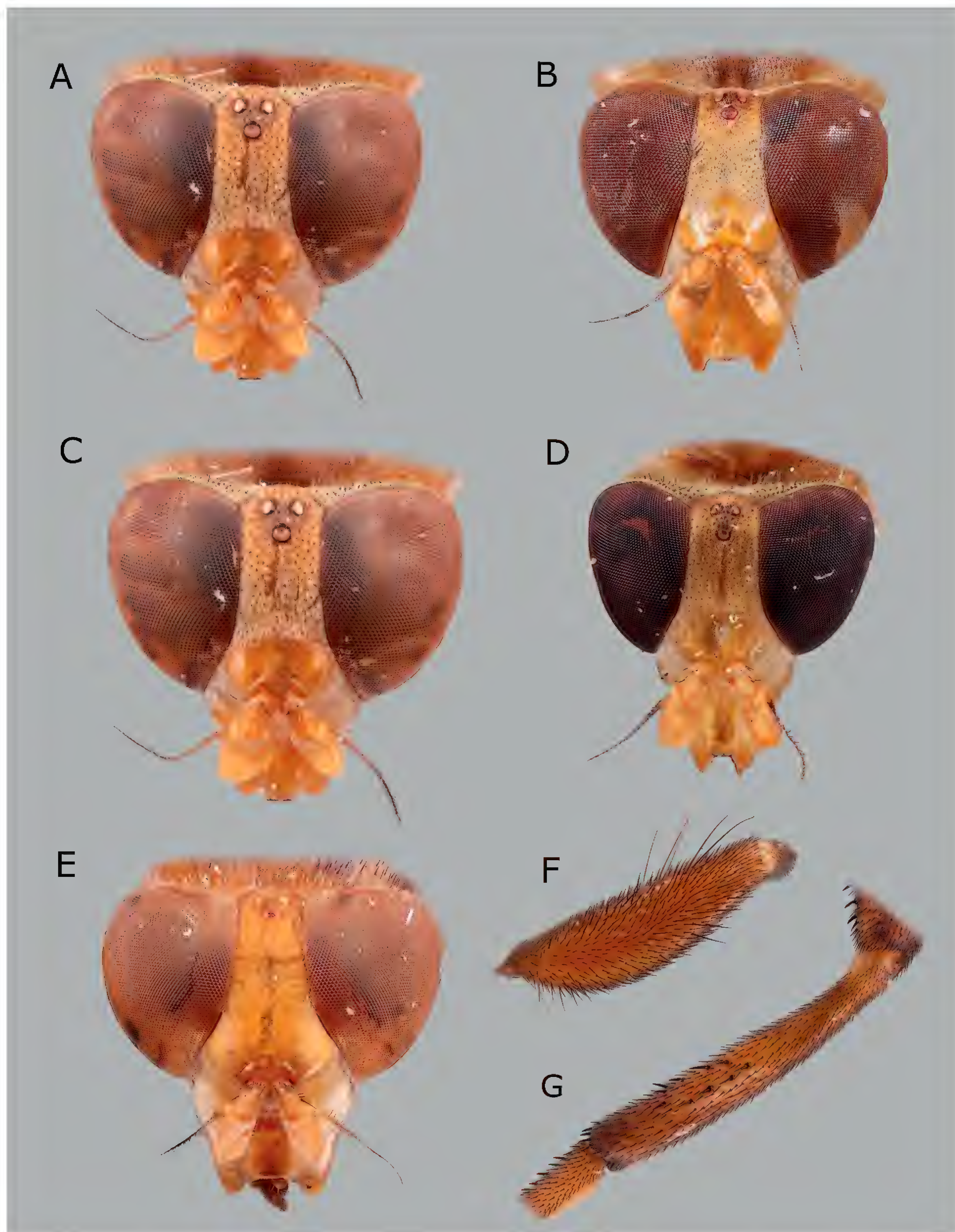


Fig. 16. *Brachyopa* and *Hammerschmidtia* species, **A–E** head female, dorsal view, **F** male profemur, dorsal view, **G** male metatibia, dorsal view. **A.** *Brachyopa obscura*, Fiby urskog, Sweden. **B.** *B. testacea*, Hautes-Fagnes, Belgium. **C.** *B. vittata*, Bolgenachtall, Germany. **D.** *B. zhelochovtsevi*, Aktru, Altay, Russian. **E.** *Hammerschmidtia ferruginea*, Fiby urskog, Sweden. **F.** *H. ferruginea*, Riikanmaa, Finland. **G.** *H. ferruginea*, Fiby urskog, Sweden.

Krivosheina (2005, 2019) are based on larvae only and it is not clear if these larvae really belong to *B. panzeri* as no adults were reared from these larvae (Speight 2020).

Adults have been seen visiting flowers of *Acer pseudo-platanus*, *Anthriscus sylvestris*, *Crataegus* spp., *Prunus padus*, *P. spinosa*, *Salix* spp., *Sambucus racemosa* L., (Barkemeyer, 1986; Röder 1990; Nilsson et al. 2007; Reemer et al. 2009) as well as on *Prunus cerasus* L. (database). Adults are more often found hovering around stumps or at sap runs on *Acer* spp., *Aesculus hippocastanum*, *Castanea sativa*, *Fagus* spp., *Pinus* spp. and *Ulmus* spp. (Torp 1994; Lauterbach 2002; Bartsch et al. 2009; Merz 2009; Ricarte et al. 2014; Mutin et al. 2016).

The flight period (Fig. 39B) is from the beginning of April until the beginning of July, with the latest date of the 20th of July. It was collected at altitudes of 0–1375 m a.s.l. (Barkemeyer 1986; Maibach et al. 1992; Ricarte et al. 2014; database). In several countries pre 1900 records are available, but several other countries only have records after 1950 to 1970. In most countries there are no records over several consecutive years and the number of records seems to have increased during the 21st century.

Population fluctuations. This species seems to fluctuate over the years in the Netherlands and has not been found in consecutive years at the same locality. The larval habitat consists of trunks and stumps of a wide variety of tree species which form a natural and rather constant factor in European forests. Thus, based on the larval habitat, it is predicted that this species will not show strong population fluctuations.

Remarks. In Western Europe this species is supposedly connected with *Fagus* forests which have provided consistent forest cover for centuries and perhaps explains why this species does not seem to fluctuate much in the number of populations (database).

Red List. In most countries treated as “Near Threatened” or “Vulnerable”, except in Germany where it is of “Least Concern”. However, in several Bundes-Länder it is classified as “Vulnerable” (Pellmann et al. 1996; Doczkal et al. 2001; Bygebjerg 2004; Dzioczek et al. 2004; Farkač et al. 2005; Ssymank et al. 2011; Artdatabanken 2019). The habitat of this species is listed as “Least Concern” in the European Red List of habitats (European Commission 2016).

Brachyopa pilosa Collin, 1939

Brachyopa pilosa Collin, 1939: 107; 3 ♂♂ syntypes NHM and 2 ♂♂ syntype in UMO, studied here. Figs 2D, 7D, 9D, 13C, 17C, 20D, 31, 39C

Distribution. A widespread European species, from northern Norway south to the Pyrenees and Italy, and

from Ireland to European Russia in the east; also known from Georgia.

Biology. Found either in rich deciduous forests (preferably *Fagus*), alluvial forests with *Populus nigra*, humid *Picea* spp. forest or even city parks (Röder 1990; Reemer et al. 2009; Ball & Morris 2014).

Larvae are found under bark of *Betula* spp., *Fagus sylvatica*, *Populus tremula*, *Quercus* spp., and *Picea abies* trunks (McLean & Stubbs 1990; Rotheray 1991; Kassebeer 1993; Torp 1994; Lauterbach 2001; Krivosheina 2005; Mielczarek et al. 2019). The species is often accompanied by larvae of the following species: *Gnophomyia viridipennis* (Gimmerthal, 1847) (Diptera: Limoniidae), *Mycetobia pallipes*, *Sylvicola cinctus* (Fabricius, 1787) (Diptera: Anisopodidae) and species of the family Sesiidae (Lepidoptera) and Ceratopogonidae (Diptera). In contrast to the known larvae of other *Brachyopa* species, there are no xylophagous larvae associated with *Brachyopa pilosa* (Krivosheina 2019). Larvae are known to be parasitized by *Tetrastichus* spp. (Hymenoptera: Eulophidae) (Kassebeer 1993). Several larvae found in a sap run on *Quercus robur* were infested by *Tetrastichus brachyopae* (van Eck et al. 2016).

Flowers visited include *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *Aegopodium podagraria*, *Allium ursinum* L., *Anemone nemorosa* L., *Anthriscus sylvestris*, *Cardamine pratensis* L., *Crataegus* spp., *Heracleum pubescens* (Hoffm.) M. Bieb., *Malus sylvestris*, *Photinia* spp., *Prunus cerasifera* Ehrh., *P. padus*, *P. spinosa*, *Pyrus communis* L., *Salix* spp. and *Viburnum opulus* L. (Torp 1973, 1994; Claussen 1985; de Buck 1990; Kormann 1993; Bygebjerg 2001; Nilsson et al. 2007; van Steenis 2016; Speight 2020) as well as *Astilbe* spp., *Cornus* spp., *Prunus avium*, *P. serotina*, *Rhamnus cathartica* L., *Spirea* spp. and *Tilia* spp. (database). Adults are found on the tree trunks of *Betula* spp., *Populus tremula*, *Quercus rubra* or the logs of coniferous trees such as *Larix* spp. and *Picea* spp. They are seldomly seen around trees with sap runs (Reemer et al. 2009).

The main flight period (Fig. 39C) is from the end of March until the end of July, with extreme dates of the 21st of February and the 24th of July, from an altitudinal range from sea level up to 1582 m a.s.l. (Maibach et al. 1992; database). In many countries this species seems to have stable populations because the number of records does not show great fluctuations over the years. In Denmark the species seems to have declined although the map is somewhat misleading as many records are from 1990 to 1999 and thus rather recent.

Population fluctuations. This species can be found during many consecutive years at the same locality and it seems unlikely that this species shows strong population fluctuations. The larval habitat consists of trunks and

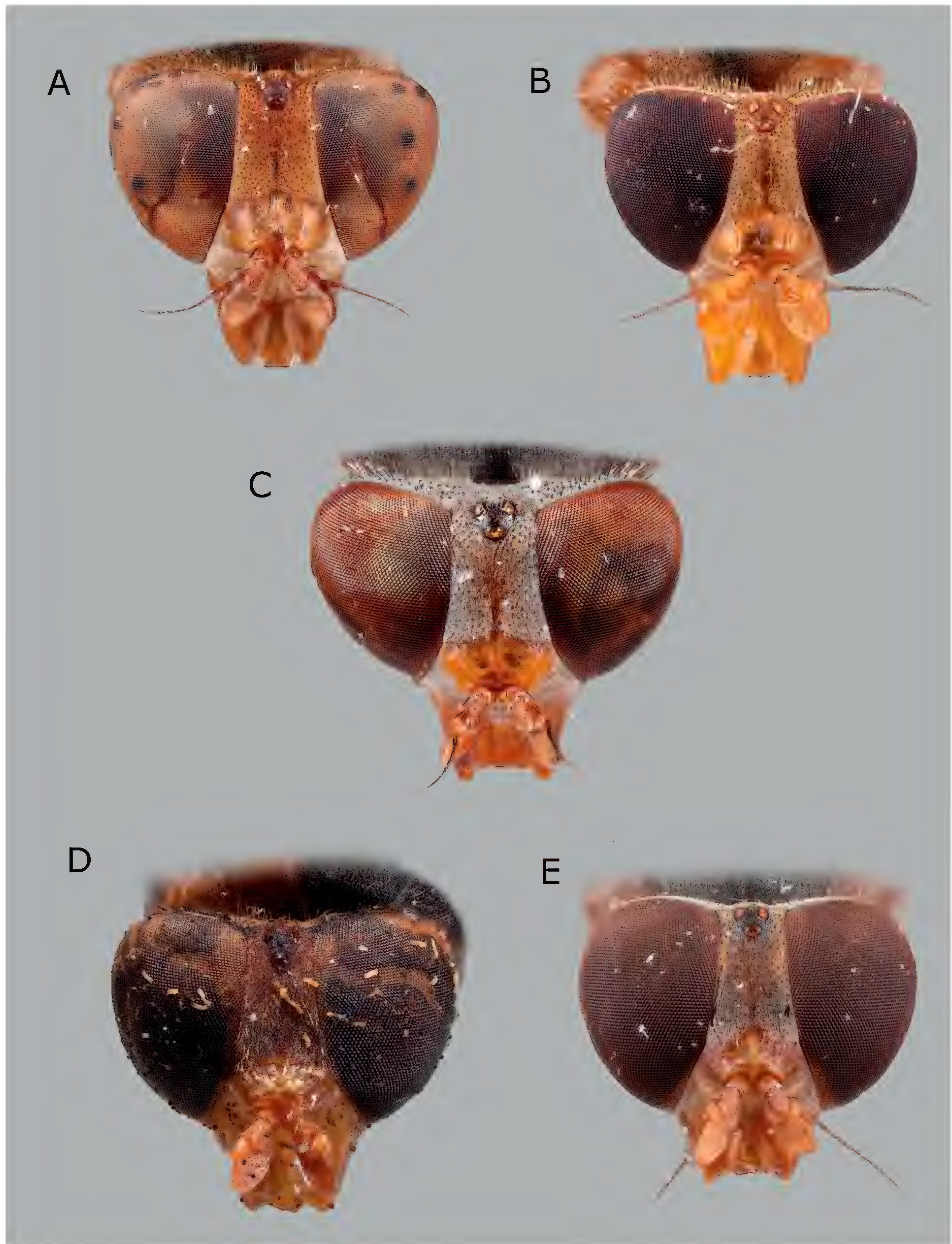


Fig. 17. Head female, dorsal view. **A.** *Brachyopa dorsata*, Fiby urskog, Sweden. **B.** *B. panzeri*, Tumnin, Russian Far East. **C.** *B. pilosa*, Fiby urskog, Sweden. **D.** *B. plena*, Zagreb, Croatia. **E.** *B. scutellaris*, Gronsveld, the Netherlands.

stumps of a wide variety of tree species which form a natural and rather constant factor in European forests.

Remarks. A widespread species possibly with good dispersal capacities because it has spread throughout the Netherlands within 50 years (Reemer et al. 2009), and colonized a small city park in an otherwise agriculture-dominated environment within some years of the felling of *Populus* spp. (J. and W. van Steenis, pers. obs.).

Red List. Mentioned in several European Red Lists and mainly categorized as “Least Concern” except in the Czech Republic (“Vulnerable”) and Norway (“Endangered”) (Bygebjerg 2004; Farkač et al. 2005; Ssymank et al. 2011; Ball & Morris 2014; Henriksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019). In Norway the species reaches its northern distributional limit which makes it vulnerable. The habitat is listed as “Least Concern”.

The wide distribution in many parts of Europe is the reason why this species is classified as “Least Concern” on other Red Lists.

Brachyopa plena Collin, 1939

Brachyopa plena Collin, 1939: 108; 2 ♂♂ syntypes in UMO, studied.

Figs 2E, 9E, 13D, 17D, 20E, 32

Distribution. A South-East European species with records from Germany (Kassebeer, 2000; Lauterbach 2002, see below) and further known from Austria, Czechia, Hungary, Slovakia and the Balkan Peninsula. This is a European endemic.

Biology. Found in Mediterranean oak forests and deciduous alluvial gallery forest within *Pinus brutia* Ten. forest (Speight 2020).

Flowers visited include *Acer campestre*, *Crataegus* spp., *Pyrus spinosa*, *Salix* spp. and *Sorbus torminalis* (Speight 2020). Adults are also seen flying around the base of *Quercus* spp. (database).

This species has been collected between the 4th of April and the 28th of May with an latest date of the 19th of July. The altitudinal range of this species is 113–1000 m a.s.l. (database). The number of records in the 21st century equals those of the 20th century and based on the strong increase in observers in the 21st century possibly indicating a slow decline.

Population fluctuations. There are no data supporting a strong fluctuation in population size or density. The larval habitat of this species is not well known. This makes it impossible to estimate if this species experiences strong population fluctuations.

Remarks. Almost identical with *B. scutellaris* that replaces this species in the western parts of Europe. The study of the type material of *B. plena* (J. van Steenis, pers. obs.) confirms the identity of the south-east European specimens as belonging to this species. The differences between these specimens and those of the western counterpart *B. scutellaris* are very small and further study is needed to see whether these species should be synonymized or kept as two separate species. Molecular data show a small difference between *B. plena* and *B. scutellaris* indicating there is some genetic variation between these species (J.H. Skevington, pers. comm.).

Red List. It is listed in Germany (Ssymank et al. 2011) as “data deficient” possibly based on the record by Lauterbach (2002). This record is very doubtful as no records of *B. scutellata*, much more common in Germany, were mentioned in Lauterbach’s paper; therefore this record is not taken into account in the present paper.

Brachyopa quadrimaculosa Thompson in Kaplan & Thompson, 1981

Brachyopa quadrimaculosa Thompson in Kaplan & Thompson, 1981: 208, ♂ holotype and ♀ allotype in ECTAU and 11 ♂♂, 2 ♀♀, in CNC, ECTAU, NHM and USNM, not studied.

Figs 4E, 4F, 11E, 11F, 15C, 18F, 33

Fig. 18. (suggested).

Distribution. Originally described from Israel with a few additional records from North Greece, the islands of Lesbos and Samos, and a first record for Cyprus (database).

Biology. Adults were found in alluvial and *Platanus orientalis* L. forest within Mediterranean *Quercus frainetto* Ten. and *Q. pubescens* forest, alluvial *Populus* forest within *Pinus brutia* forest and Mediterranean maquis. Found visiting flowers of *Pyrus spinosa* and *Smyrniolum olusatrum* L. (Kaplan & Thompson 1981; Speight 2020). Also collected in alluvial *Alnus orientalis* forest within mixed *Platanus orientalis* and *Pinus brutia* forest (collection A. van Eck).

The flight period is from the 31st of March until the 1st of May and the species is collected at altitudes of 25–550 m a.s.l. (database). The first European record dates back to 1988 and all other records are from 2007 or later.

Population fluctuations. Too little is known about the habitat preferences of this species to say anything about the population fluctuations.

Remarks. This species is most likely to have the same habitat preferences as *Brachyopa minima*, and is likely to be affected by the same habitat threats on Greek islands,

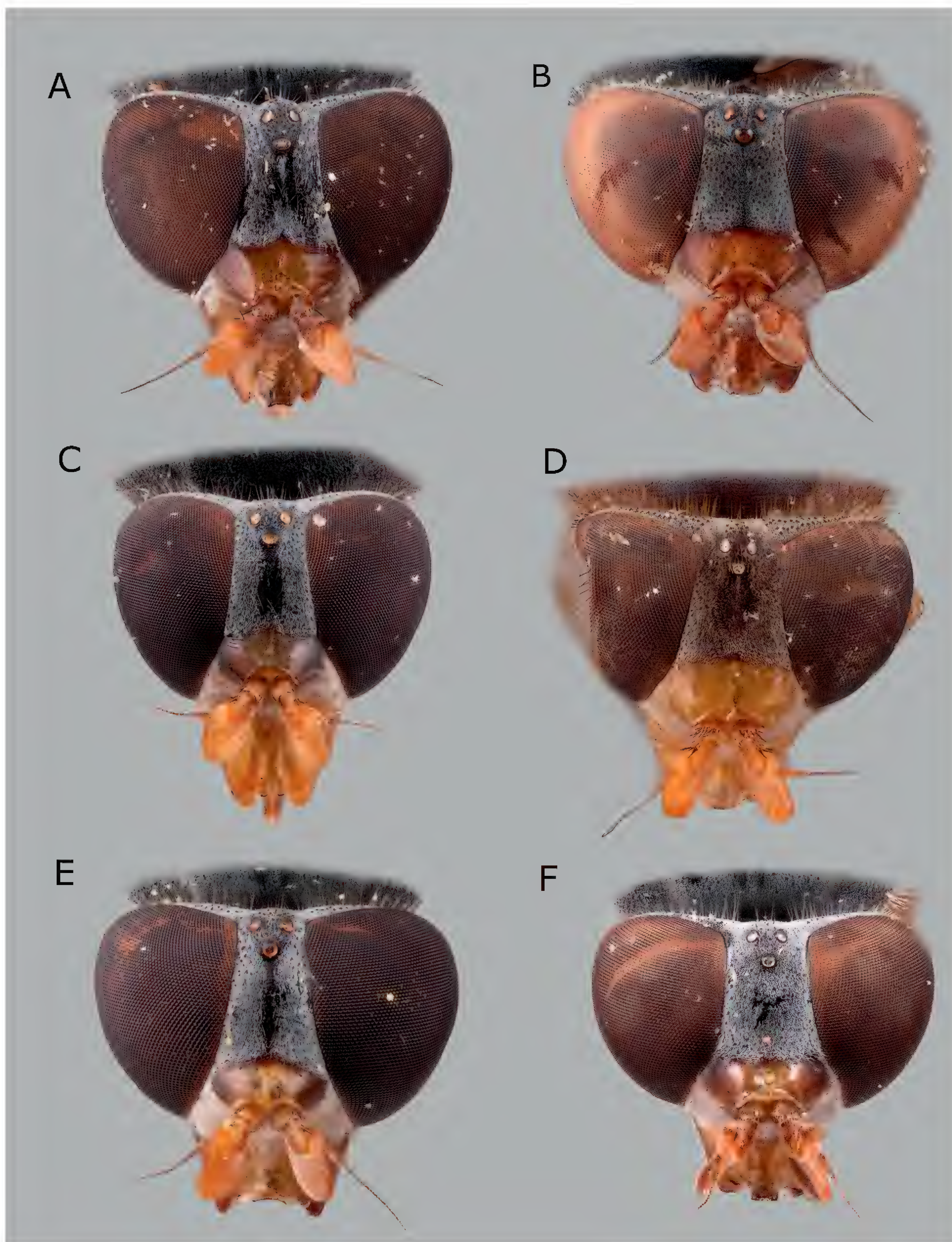


Fig. 18. Head female, dorsal view. **A.** *Brachyopa atlantea*, female, Granada, Spain. **B.** *B. bicolor*, Maarn, the Netherlands. **C.** *B. bimaculosa*, Arkadia, Greece. **D.** *B. cinerea*, Komsomolsk-na-Amur, Russian Far East. **E.** *B. insensilis*, Novi Sad, Serbia. **F.** *B. quadrimaculosa*, Samos, Greece.

namely sheep grazing (Kizos et al. 2013) and forest fires (Kalabokidis et al. 2013).

Red List. Not mentioned on any Red List. See further comment under *Brachyopa minima*.

***Brachyopa scutellaris* Robineau-Desvoidy, 1844**

Brachyopa scutellaris Robineau-Desvoidy, 1844: 39; ♀ holotype in MNHNP, not studied.
Figs 2F, 7E, 9F, 13E, 17E, 20F, 32, 39D

Distribution. A west European species, regarded as European endemic.

Biology. Found in humid deciduous forests, most notably alluvial and swamp forests.

Larvae are found in sap runs on *Acer pseudoplatanus*, *Alnus* spp., *Fraxinus excelsior*, *Populus tremula*, *Taxus baccata* L. and *Ulmus glabra* (Seguy 1961; Rotheray 1996; Pellmann 1998; Reemer et al. 2009). In a sap run on *Fraxinus excelsior* in Bretagne, France, the larvae of this species were accompanied by larvae of *Ferdinandea cuprea* Scopoli and *Volucella inflata* Fabricius (Diptera: Syrphidae) (J. van Steenis, pers. obs.).

Visiting flowers of *Aegopodium podagraria*, *Anthriscus sylvestris*, *Cardamine pratensis*, *Cornus* spp., *Crataegus* spp., *Heracleum Malus* spp., *Photinia* spp., *Prunus padus*, *Rubus fruticosus*, *Sorbus* spp. and *Viburnum opulus* (de Buck 1990; Bygebjerg 2001; Reemer et al. 2009; Mielczarek et al. 2019), as well as *Acer* spp., *Chaerophyllum temulum* L., *Genista* spp., *Heracleum* spp., *Prunus serotina*, *Salix* spp. and *Smyrniolum olusatrum* (database). Adults are more often found on tree trunks of *Fagus* spp., *Quercus* spp., and sap runs on *Betula* spp. or hovering around *Castanea sativa* (Ricarte et al. 2014), and around *Acer* spp. (database).

The flight period (Fig. 39D) is from the beginning of April until end of July with the extreme dates of the 20th of March and the 20th of August (database). A species found at altitudes of 0–1250 m a.s.l. (Maibach et al. 1992; Ricarte et al. 2014; database). In France and Great Britain this species shows large fluctuations in the number of records each year, while in several other countries the number of records seems to be more stable.

Population fluctuations. This species can be found in the same locality several years in a row, sometimes even in forests seemingly without suitable external sap-runs. The larvae are mostly associated with external sap-runs, a habitat showing extreme fluctuations over time. This makes this species will very likely also show strong population fluctuations.

Remarks. In Poland, large variation in the size and shape of the sensory pit was found (Mielczarek et al. 2019), which could indicate that *Brachyopa plena* is just a vari-

ant of *B. scutellaris* and not a separate species. There are also other scenarios possible and the area where these specimens were found would be the place to visit for further study, to see if there is overlap in the distinguishing characteristics between these two species.

Red List. Mentioned on several regional Red Lists under “Near Threatened”, “Vulnerable” and even “Endangered” (Bygebjerg 2004; Farkač et al. 2005; Ssymank et al. 2011). In Sweden it is listed as “not applicable” (Artdatabanken 2019) but the reason why is not very clear; its real threat category for Sweden could be “Near Threatened” to “Endangered”. The corresponding habitat types in the EU list are, with the threat category in brackets G1.2a (LC), G1.2b (EN) and G1.4 (VU) (European Commission 2016).

***Brachyopa silviae* Doczkal & Dziock, 2004**

Brachyopa silviae Doczkal & Dziock, 2004: 50; ♂ holotype in NMM, 2 ♂♂, 3 ♀♀ paratypes in private collections, not studied.
Figs 4B, 11B, 33

Distribution. Known from its type locality in Germany and recently reported from France and Serbia (Doczkal & Dziock 2004; Speight et al. 2013; van Steenis et al. 2019) and also known from Austria. It is an endemic species for Europe.

Biology. Found near sap runs on a trunk of a *Carpinus betulus* tree and in ancient *Quercus-Fagus* forests (van Steenis et al. 2019) as well as in thermophilous *Quercus* and mesophilous *Fagus* forests (Doczkal & Dziock 2004; Speight et al. 2013).

Visiting flowers of *Crataegus* spp. and *Pyrus spinosa* (Speight 2020) and *Acer pseudoplatanus* (database).

The species has been collected between the 3rd of April and the 12th of May at an altitude of 75–925 m a.s.l. (database). All 10 records are post 1999.

Population fluctuations. This species has only observed regularly in Germany. The records for Austria, France and Serbia were mostly single specimens on a single occasion. The German records are too few to see any sign of extreme fluctuations.

Remarks. This is a very rare species found in three widely separated locations. Only the German population can be considered to be stable. The localities are so far apart that there will not be any exchange between them and, as such, the distribution is extremely fragmented.

Red List. Only mentioned on the German Red List, classified as “data deficient” (Ssymank et al. 2011).

***Brachyopa testacea* (Fallén, 1817)**

Rhingia testacea Fallén, 1817: 34, types in NHRS, not studied.

Figs 1B, 8B, 12B, 16B, 19B, 34, 40A

Distribution. A widespread boreo-alpine species found from northern Norway south to the Pyrenees and Bulgaria and from Belgium east through the Alps and the Baltic states into European Russia. It is also widely distributed in the boreal zone of the Palaearctic region up to the Russian Far East.

Biology. The adult habitat consists of pine forests or pine-dominated mixed forests (Löhr 1992; Bartsch et al. 2009; Reemer et al. 2009). Adults are also observed in broadleaved dominated mixed forests, often while visiting flowers (database).

Larvae and puparia have been found under bark of *Picea* stumps in association with tunnels of Lymexylidae larvae (Coleoptera) (Nielsen 1992; Löhr 2002; Bartsch et al. 2009; Krivosheina 2019).

Adults are often found near damaged coniferous trees, especially stumps of *Picea abies* (Löhr 1992; Mutin et al. 2016) but also further away from coniferous trees in mixed forests foraging on flowering herbs and shrubs of *Prunus padus* and *Sorbus aucuparia* L. (J. van Steenis, pers. obs.). Other flowers visited are *Acer pseudo-platanus*, *Aegopodium podagraria*, *Anemone nemorosa*, *Angelica archangelica* L., *Angelica sylvestris* L., *Anthriscus sylvestris*, *Cardaminopsis arenosa* (L.) Lawalrée, *Crataegus* spp., *Malus* spp., *Meum* spp., *Myrrhis odorata* (L.) Scop. *Prunus avium* (as *Cerasus avium* in part of database), *P. spinosa*, *Ribes alpinum*, *Salix* spp., *Saxifraga granulata* L., *Scorzonera humilis* L., *Stellaria holostea* L., *Taraxacum* spp., *Valeriana* spp. and *Viburnum opulus* (Torp 1994; Bartsch et al. 2009; Speight 2020) and *Pimpinella major* (L.) Huds. and *Spirea* spp. (database).

The main flight period (Fig. 40A) is from the middle of April until the end of July with extreme dates of the 2nd of April and 21st of August. Found at altitudes from sea level up to 1880 m a.s.l. (database). In all countries recorded extensively during the 21st century, but no recent records from Denmark (since 1999) and Switzerland (since 1996).

Population fluctuations. This species is dependent on pine forests. The larvae are dependent on rather freshly cut stumps. This habitat is heavily managed and will produce a constant amount of suitable larval habitat due to regular tree felling. It seems this species does not show strong population fluctuations.

Red List. This species is listed as “Least Concern” on all regional Red Lists and also its habitat does not seem to be threatened (Bygebjerg 2004; Ssymank et al. 2011;

Henriksen & Hilmo 2015; European Commission 2016; Artdatabanken 2019; Hyvärinen et al. 2019).

***Brachyopa vernalis* Van Steenis & Van Steenis, 2014**

Brachyopa vernalis Van Steenis & Van Steenis, 2014: 13; ♂ holotype in NBC, 7 ♂♂ paratypes in NBC, PJSA, PMRL, PWSB, FSUNS, ZMUC, all types studied.

Figs 4D, 11D, 15D, 22

Distribution. Only known from three localities on Crete (Greece), based on material collected in 1997, 2008 (van Steenis & van Steenis 2014) and 2012, and hence a European endemic.

Biology. Found visiting flowers of *Crataegus* spp. and *Prunus* spp. in Mediterranean deciduous forests and in a forested part of a deep ravine.

This species was collected on the 28th of March, the 8th of April and the 8th of May at an altitudinal range of 350–900 m a.s.l. (database).

Population fluctuations. Nothing can be concluded based on the data we have here, but as seen for some other Mediterranean species of *Brachyopa*, its larvae are most likely living in sap runs and as such, prone to show large population fluctuations.

Remarks. Crete has been visited by renowned dipteran collectors (Jan Lucas, Claus Claussen, etc.) in the past and only recently nine specimens of this species have been collected, indicating it should be classified as an extremely rare species. It has been recorded at three localities in Crete, all in forested habitats. Only one locality is within a protected area. As in many Mediterranean areas this habitat is under threat due to overgrazing and forest fires. This in combination with the restricted range of occurrence makes this species very vulnerable to extinction.

Red List. Not mentioned on any Red List but, due to its restricted distribution and the threats to its habitat, a candidate to be listed in one of the IUCN threat categories.

***Brachyopa vittata* Zetterstedt, 1843**

Brachyopa vittata Zetterstedt, 1843: 687; type in ZIL, not studied.

Figs 1C, 7F, 8C, 12C, 16C, 19C, 35, 40B

Distribution. A widespread species found from northern Sweden south to the Pyrenees and northern Greece and from the Netherlands east into European Russia and further to the Russian Far East and Japan.

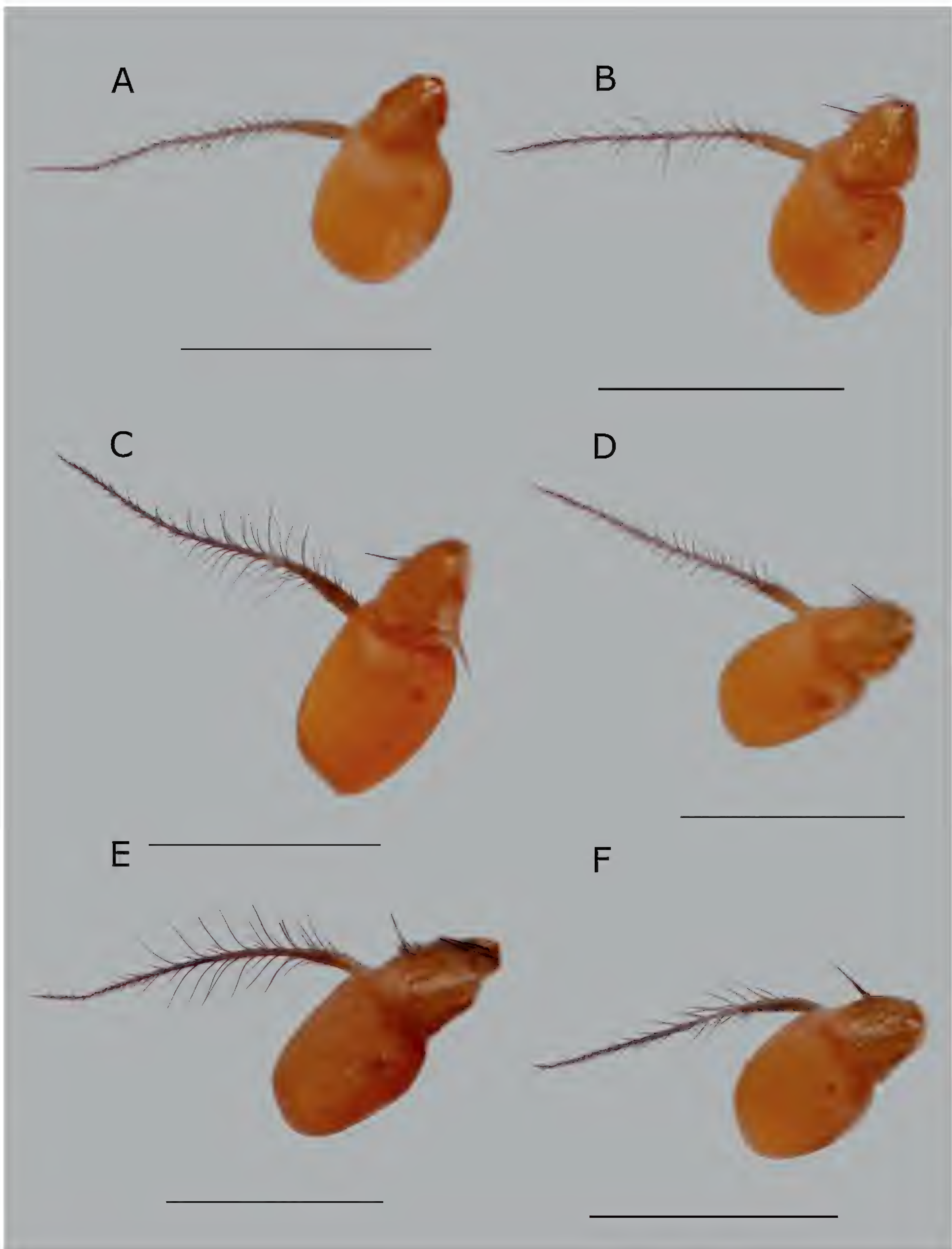


Fig. 19. Basoflagellomere male, medio-lateral view. **A.** *Brachyopa obscura*, Hågadalen, Sweden. **B.** *B. testacea*, Bolgenachtall, Germany. **C.** *B. vittata*, Belchen, Germany. **D.** *B. zhelochovtsevi*, Aktru, Altay, Russia. **E.** *Hammerschmidtia ferruginea*, Hinteralfeld, France. **F.** *H. ingrlica*, Tuva, Russia.

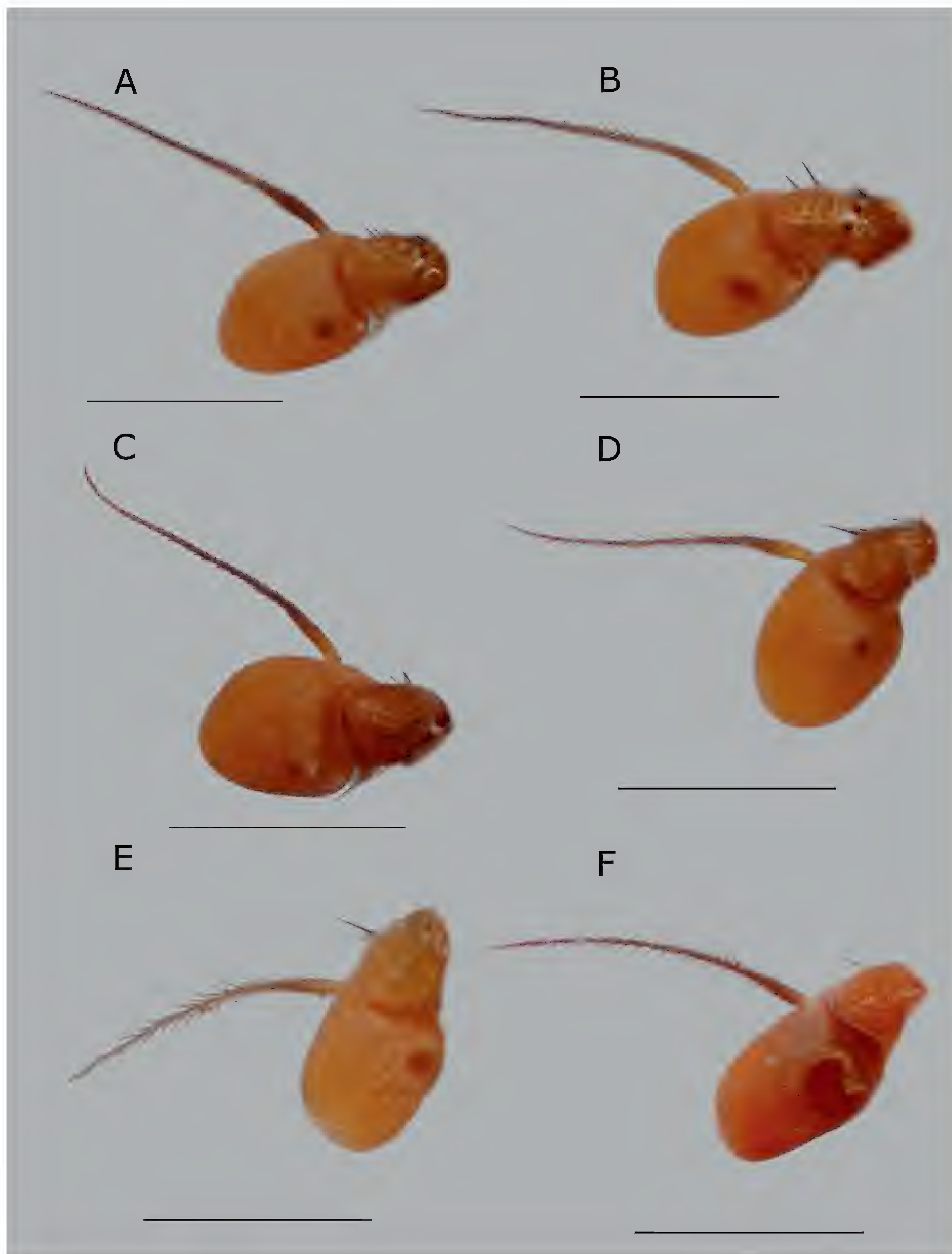


Fig. 20. Basoflagellomere male, medio-lateral view. **A.** *Brachyopa dorsata*, Belchen, Germany. **B.** *B. panzeri*, Dresden, Germany. **C.** *B. maculipennis*, Novi Sad, Serbia. **D.** *B. pilosa*, Valkenburg, the Netherlands. **E.** *B. plena*, Kalavryta, Greece. **F.** *B. scutellaris*, Cadier en Keer, the Netherlands.

Biology. Adult habitat is old growth *Picea* and *Pinus* forests but also found in mixed swamp forest (Löhr 1992; Bartsch et al. 2009; Reemer et al. 2009).

Larvae live in *Picea* spp. and *Larix* spp. stumps as well as in standing trunks and stumps of *Abies* spp. with tunnels of *Hylecoetus flabellicornis* (Coleoptera: Lymexylidae), *Trypodendron lineatum*, *Ips sexdentatus* (Boerner, 1767) (Coleoptera: Curculionidae) and *Zabrachia minutissima* (Zetterstedt, 1838) (Diptera: Stratiomyidae). They are also accompanied by the saprophagous larvae of *Sylvicola cinctus* (Diptera: Anisopodidae) (Krivosheina 2005, 2019).

Flowers visited include *Aegopodium podagraria*, *Anthriscus sylvestris*, *Caltha palustris*, *Crataegus laevigata*, *Crataegus monogyna*, *Prunus avium*, *P. padus*, *Salix* spp., *Sambucus nigra* L., *S. racemosa*, *Sorbus aucuparia* and *Viburnum* spp. (Séguy 1961; Barkemeyer 1986; de Buck 1990; Röder 1990; Nielsen 1992; van Steenis 2011; Speight 2020), as well as *Alliaria petiolata*, *Pimpinella major*, *Spirea* spp. and *Valeriana officinalis* L. (database). Adults are found on tree stumps and trunks of a wide range of coniferous trees.

The flight period (Fig. 40B) is from the middle of April until the middle of August (database). The altitudinal range of this species is 10–2270 m a.s.l. (Barkemeyer 1986; Maibach et al. 1992; database). This species has been recorded during all time periods in France and Germany and in many other countries regularly after its first discovery. Only in Sweden it was recorded around 1900 with the next records from 1999, 2009 and 2013, indicating strong population fluctuations.

Population fluctuations. As indicated for *Brachyopa testacea*, this is a species dependent upon pine forests and, as larvae, on rather freshly cut stumps. This habitat is heavily managed and will produce a constant amount of suitable larval habitat due to regular tree felling. It seems this species does not show strong population fluctuations in its central distributional range.

Remarks. This is a species of coniferous forests often found near trunks and stumps defending a territory.

Red List. This species is listed from “Least Concern” to “Endangered” on the regional Red Lists (Ssymanek et al. 2011; Henriksen & Hilmo 2015; Artdatabanken 2019). In Finland it is listed as “data deficient” (Hyvärinen et al. 2019). These categories contrast strongly with one another because there are only very few records for each country and most of these are from recent times, except in Sweden where there are some very old records and some recent ones too, indicating a possible absence of many years. The species seems to be at its northern limits in these countries, so the threat category seems to depend on how important you judge the local populations. The species should either be categorized as “data deficient”

in all three countries or in one of the threat categories “Vulnerable” to “Critically Endangered”. In Central Europe the species seems to be widespread with stable populations, and its habitat is classified as “Least Concern” (European Commission 2016), so there seem to be significant differences in the threat category between Fennoscandia and the rest of Europe.

***Brachyopa zhelochovtsevi* Mutin, 1998**

Brachyopa zhelochovtsevi Mutin, 1998: 4; ♂ holotype in ZMSU, studied.

Figs 1D, 8D, 12D, 16D, 19D, 33

Distribution. Only known in Europe from two Finnish records for this otherwise East-Palaeartic species, with some records from the Altai.

Biology. Found in an ancient forest with fallen logs of *Abies* spp., *Betula* spp. and *Populus tremula* (Haarto & Kerppola 2009). Adults found near damaged coniferous trees (Mutin et al. 2016). Flowers visited *Ledum palustre* L. (Speight 2020).

Collected on the 24th and the 29th of June and on the 13th of July. One old record from 1911 and the other two from 2008 (database).

Population fluctuations. Nothing can be concluded concerning fluctuations in population size.

Remarks. This species is very similar to both *B. obscura* and *B. testacea*, and is easily overlooked in the field, although *B. obscura* tends to be the more light-coloured and *B. zhelochovtsevi* the most dark-coloured species. The distribution of this species could be wider than currently known. As very little is known about its adult and larval habitat no conclusions can be drawn on possible threats.

Red List. For Finland the species is categorised as “data deficient” (Hyvärinen et al. 2019).

The European species of the genus *Hammerschmidtia*

***Hammerschmidtia ferruginea* (Fallén, 1817)**

Rhingia ferruginea Fallén, 1817: 34; type in NHRS, not studied.

Hammerschmidtia vittata Schummel, 1834: 740; type in NMW, (syn by Peck 1988), not studied.

Figs 1E, 6A, 8E, 12E, 16E–G, 19E, 36, 40C

Distribution. A widespread species found from northern Norway south to the Pyrenees and from central France east through the Alps, the Balkan Peninsula and Poland to European Russia. Also known from Scotland and Georgia and further east to the Russian Far East. The re-

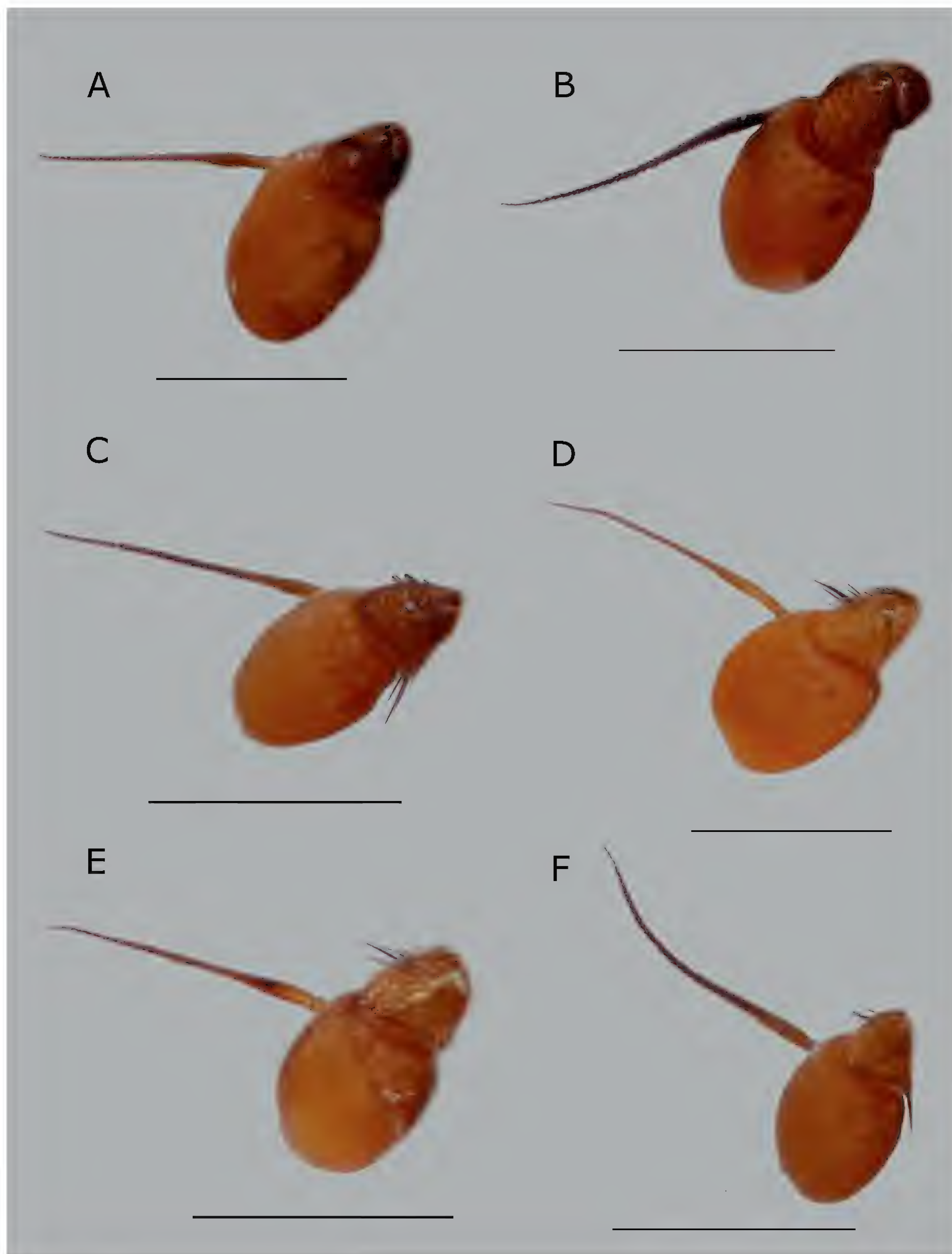


Fig. 21. Basoflagellomere, medio-lateral view **A.** *Brachyopa atlantea*, female, Granada, Spain. **B.** *B. bicolor*, male, Arkadia, Greece. **C.** *B. bimaculosa*, male, Arkadia, Greece. **D.** *B. cinerea*, female, Komsomolsk-na-Amur, Russian Far East. **E.** *B. grunewaldensis*, male, Arkadia, Greece. **F.** *B. insensilis*, male, Novi Sad, Serbia.

cord in NW France (Séguy, 1961) is a strange record and needs verification.

Biology. The adult habitat consists of pine and birch taiga in Scandinavia and Scotland, and mixed alpine forests up to 1200 m a.s.l. with large stands of *Populus tremula* (Nielsen 1992; Rotheray & McGowan 2000; Bartsch et al. 2009).

The larval habitat has been intensively studied in Scotland and consists of sap accumulations in fallen logs of *Populus tremula* or sap runs on the same tree (Rotheray 1991; Rotheray & McGowan 2000; Rotheray et al. 2009, 2014). The larvae live in recently fallen logs with sappy decay, which lasts for 2 to 3 years. From one such log almost 1000 specimens were collected in emergency traps (Rotheray et al. 2014). In other parts of the world larvae have been found in similar conditions (Krivosheina 2003).

Adults visit flowers of *Aegopodium podagraria*, *Angelica sylvestris*, *Anthriscus sylvestris*, *Conopodium majus* (Gouan) Loret, *Crataegus* spp., *Prunus padus*, *Pyrus communis*, *Ranunculus acris* L., *Rosa* spp., *Rubus fruticosus*, *Salix* spp., *Sorbus aucuparia*, *Syringa* spp. and *Valeriana* spp. (de Buck 1990; Röder 1990; Nielsen 1992; Stubbs & Falk 1996; Nilsson et al. 2007; Ball & Morris 2014; Speight 2020), as well as *Chaerophyllum temulum*, *Filipendula ulmaria*, *Heracleum sphondylium* L., *Malus sylvestris*, *Prunus laurocerasus* L., *Sambucus nigra*, *Spirea* spp. and *Viburnum opulus* (database).

Its flight period (Fig. 40C) is from the end of April until the beginning of August with extreme dates of the 2nd of April and the 19th of August. This species is found at altitudes of 20–1925 m a.s.l. (database).

Population fluctuations. Extreme fluctuations were found in the Scottish Highlands (Rotheray et al. 2008; Ball & Morris 2014) and based on its larval biology it is highly likely this species shows fluctuations over its entire distributional range.

Remarks. This is a very characteristic species which is unlikely to be overlooked in the field due to its size and preference for flowering Apiaceae as an adult food source.

Red List. In northern countries this species is listed as “Least Concern” (Henriksen & Hilmo 2015; Artdatabanken 2019; Hyvärinen et al. 2019), while it is “Endangered” to “Critically Endangered” in Germany and Great Britain (Ssymank et al. 2011; Ball & Morris 2014). In Scotland conservation actions are in place (Rotheray et al. 2008), and these actions will probably have a positive impact on its occurrence in Great Britain.

In other parts of Europe, the specific habitat of the species falls within EUNIS category G1.4 or possibly G1.9 and G4.8 of which G1.4 is considered “Vulnerable”

(European Commission 2016). In light of this, *Hammerschmidtia ferruginea* could also be threatened and would possibly classify under the same category although the species is not considered threatened in the Balkan Peninsula (Vujić et al. 2001).

Hammerschmidtia ingrlica Stackelberg, 1952

Hammerschmidtia ingrlica Stackelberg, 1952: 37; ♂ holotype and 2 ♂♂, 1 ♀ paratypes in ZISP, studied. Figs 1F, 5C, 6B, 8F, 12F, 19F, 37

Distribution. Described from European Russia with many records from the surroundings of St Petersburg and Moscow (Stackelberg 1952, database), and with a range extending eastwards to the Russian Far East. (Mutin et al. 2016). Recently recorded in Finland.

Biology. Adults are found in mixed boreal forests with overmature deciduous trees (Krivosheina 2003; Mutin et al. 2016).

The larvae are found in sap accumulations under the bark of *Juglans mandshurica* Maxim., *Populus tremula* and *Ulmus* spp. (Krivosheina 2003). Adults were collected in an emergence trap on a *Populus tremula* trunk (Polevoi et al. 2018).

In the Russian Far East, it was found visiting flowers of *Cornus alba* (as *Swida alba* in Mutin et al. 2016).

The flight period in Europe is from the 25th of April until the 30th of June at altitudes between 25 and 400 m a.s.l. (database).

Population fluctuations. The larvae seem to have similar habitat preferences to *Hammerschmidtia ferruginea*. It is likely that both *Hammerschmidtia* species show similar population fluctuations.

Remarks. The Finnish island where this species was found is a former Soviet Military base, and several plant species have been found there which originate from Russia. It is hypothesized that *H. ingrlica* is an introduced species now maintaining a population on the island (Kerppola 2011). However, this is questionable because it occurs in the nearby European part of Russia, and similar habitats occur on both sides of the border.

It seems that the Nearctic *Hammerschmidtia rufa* Williston, 1882 and eastern-Palaeartic specimens of *H. ingrlica* have identical DNA, and thus it is proposed that *H. ingrlica* should be a junior synonym of the older name *H. rufa* (Skevington et al. 2019). This synonymy was proposed in a field guide without mentioning the descriptive authority, nor has the type of *H. ingrlica* been studied, and so this change is not applied here.

Red List. As a supposed non-native species to Finland, it is listed as “not applicable” in the Red List of this country (Hyvärinen et al. 2019).

DISCUSSION

This discussion will focus on the results given under each species and summarize this in a generalized way. For ease of reading no references are given here. The discussion focuses on the current knowledge and especially gaps which need to be investigated more thoroughly to understand more fully the possible effects of changing habitat on population dynamics of the species.

The species of the genera *Brachyopa* and *Hammerschmidtia* are highly specialized in their larval habitat. In general, different kinds of tree sap accumulations form the larval habitat. This can be external sap runs caused by physical damage or other larvae, or internal accumulations of sap under bark of stumps or fallen logs. Most of these habitats are within living trees, but accumulations of sap on recently felled trees are also used by some species. This habitat is restricted by a variety of factors and its availability could fluctuate greatly over time. The amount of suitable larval habitat increases after storms, fires, infectious outbreaks causing damage to trees or felling activity by forestry. These fluctuations are mostly random and hard to predict, causing large fluctuations in population densities. Moreover, each year, the sap-runs tend to dry out in autumn, making survival of the larvae a challenging process. Consequently, adaptations have evolved in response to these uncertainties. The extensive longevity and high desiccation tolerance in the larval stage help to overcome the yearly fluctuations. The longevity can also span the period of tree recovery when little larval habitat is present. Other strategies involve the adults, and probably include high mobility and the ability to identify the larval habitat at great distances, especially in the females.

Within the genus *Brachyopa* there are basically two larval biotopes, and species tend to have a preference for either one. Some species are generalists, with larvae occurring in a wide range of deciduous and coniferous trees, whilst others tend to occur only in coniferous trees. The latter are mostly larvae living in sap accumulations under bark of stumps and trunks, perhaps a more stable habitat than sap runs on living trees. The sap-run-dependent species tend to have a wider range of host trees, including deciduous and coniferous trees, although it seems they do have some preference, for instance, *Quercus* spp. being preferred by *Brachyopa bicolor* and *Aesculus hippocastanum* by *B. insensilis*.

Most knowledge about larval habitat is gathered from field observations rather than through extensive ecological or behavioural studies. Only *Hammerschmidtia ferruginea*, a true specialist on accumulations of sap under bark of recently felled *Populus tremula* logs, has been investigated in great detail. These studies suggested the minimal forest area needed for survival as being at least 15 ha with large stands of *Populus tremula* in all life stages. All other species need to be investigated as thorough-

ly as *H. ferruginea* in order to establish what tree species are needed, how large the forest area should be and how near other forests need to be in order to ensure their future survival.

It seems that no species of *Brachyopa* or *Hammerschmidtia* have become extinct in Europe yet. Two very rare species in Europe (*Brachyopa atlantea* and *B. zhelochovtsevi*) could be relicts with a larger range in the past. Two other species (*Brachyopa testacea* and *B. vittata*) could have benefitted from the increasing area of coniferous plantations in Western Europe. Most of the species dependent upon deciduous forests have extended their ranges northwards since the last ice age, along with the reforestation of Europe in this period. The species thus seem to be able to adapt to a changing environment, but we do not know how quickly they are able to do this and whether they will be able to continue to thrive as habitat changes accelerate due to global warming and other human impacts.

In this paper we have compiled all information available to us and have provided data on distribution, habitat, ecology, habitat threats and possible population fluctuations. This could serve as a basis for compiling a nationwide or regional Red List and, most of all, to encourage biologists to do more research on the ecology of the species of these two genera.

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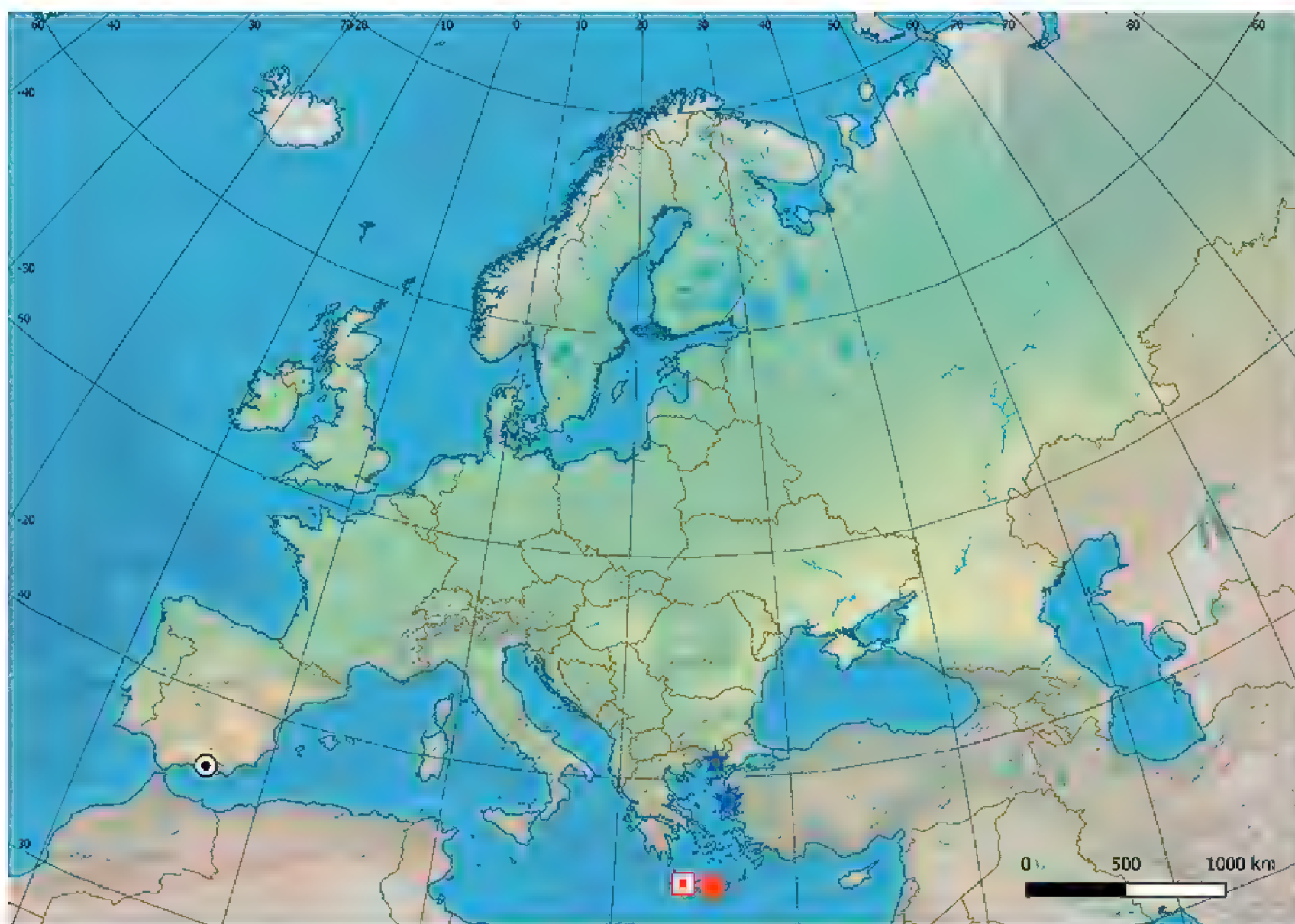


Fig. 22. Distribution map. *Brachyopa atlantea*, dot; *B. minima*, star; *B. vernalis*, square. (white <1950, white with black point ≥1950 <2000, black ≥2000).

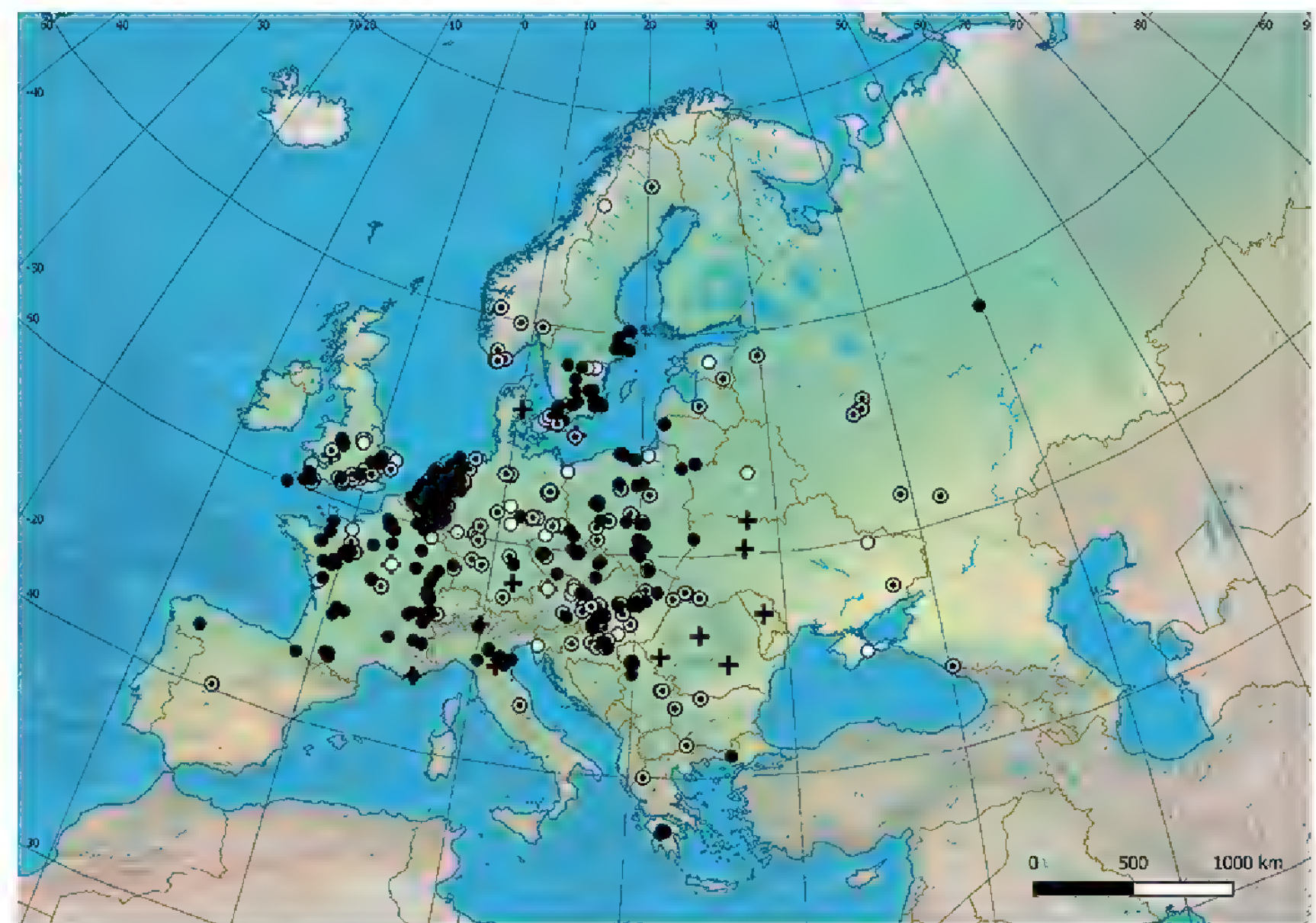


Fig. 23. Distribution map. *Brachyopa bicolor* (white <1950, white with black point ≥1950 <2000, black ≥2000, + datum unknown).

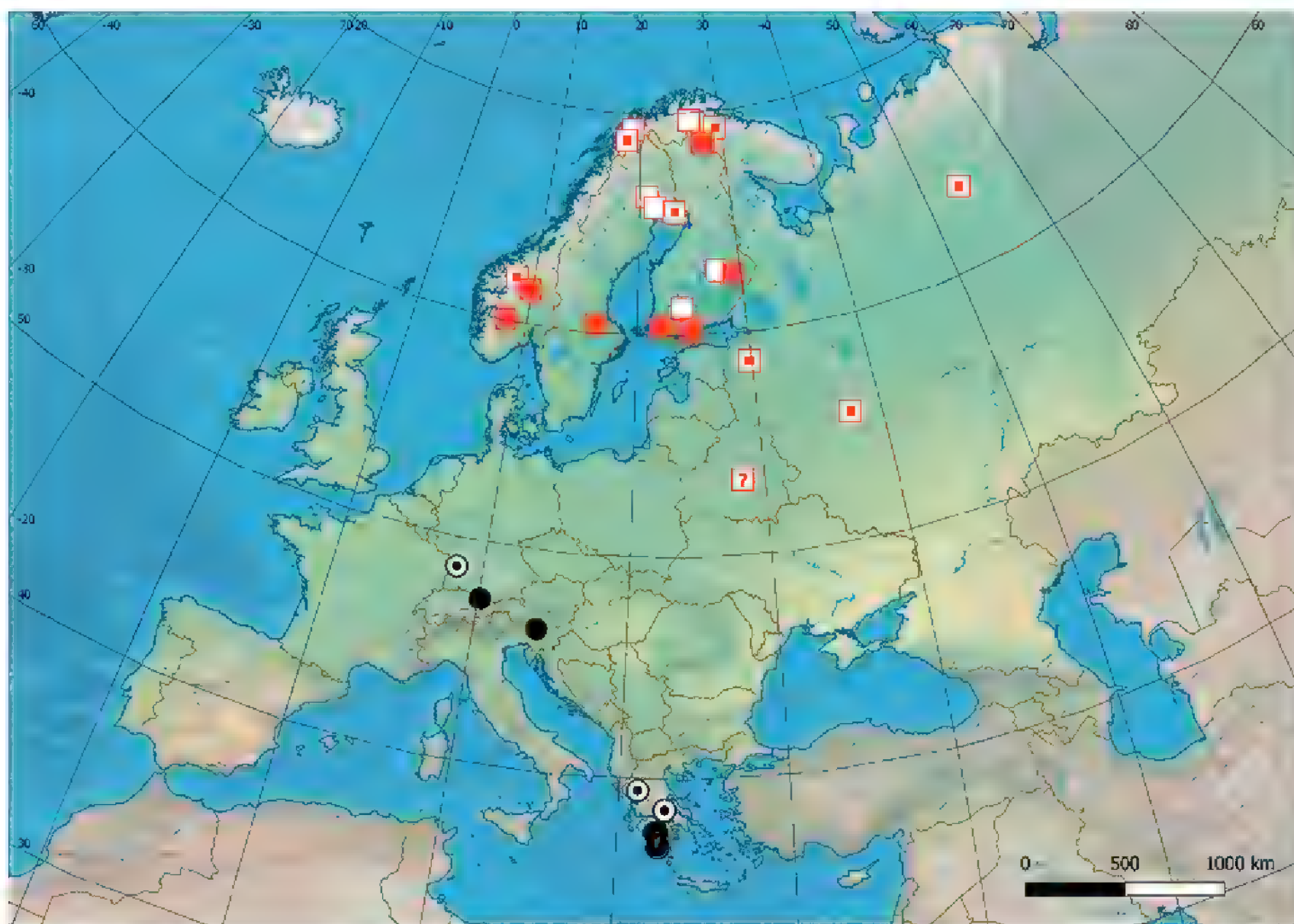


Fig. 24. Distribution map. *Brachyopa bimaculosa*, dot; *B. cinerea*, square. (white <1950, white with black point ≥1950 <2000, black ≥2000, ? = uncertain record).

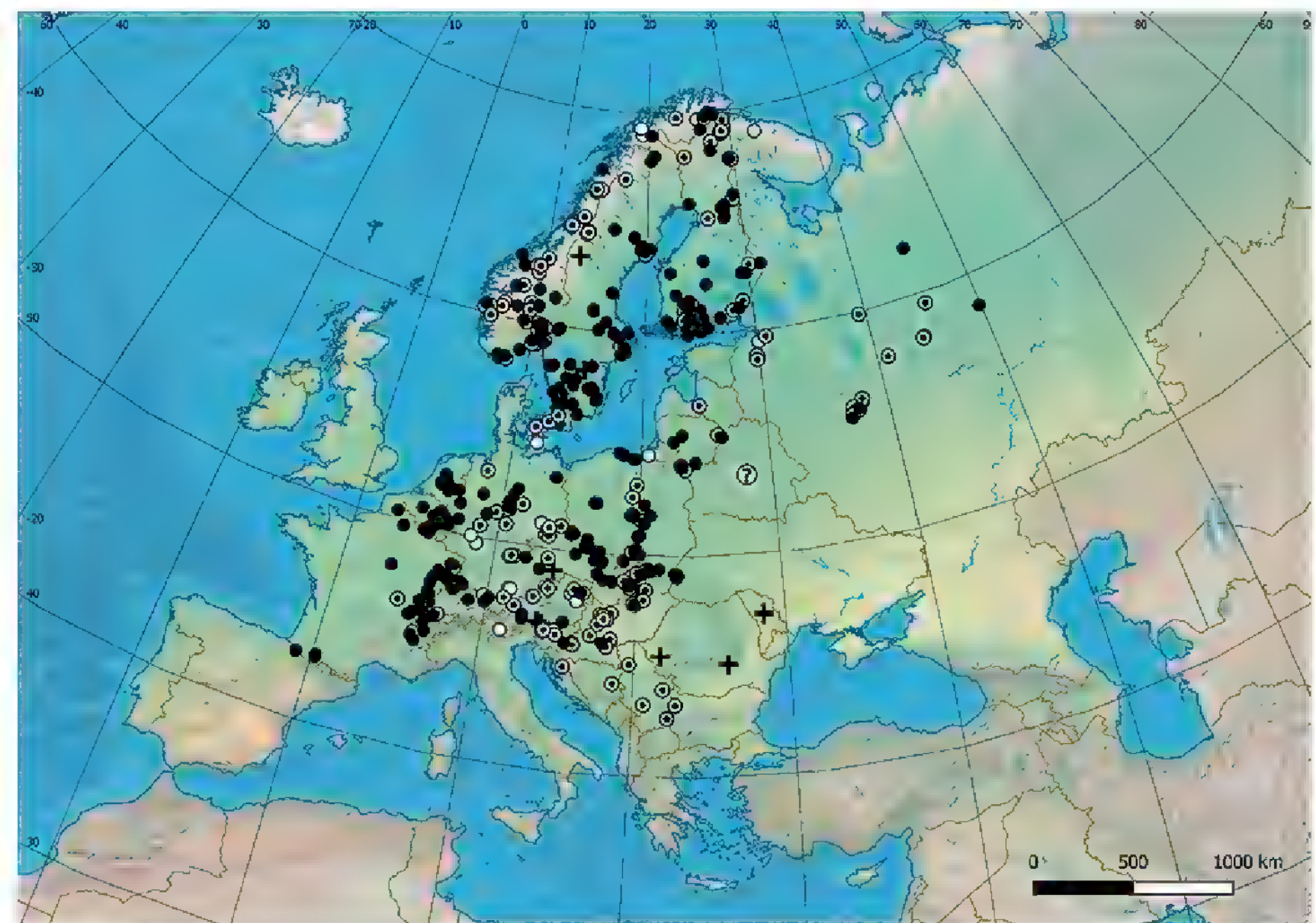


Fig. 25. Distribution map. *Brachyopa dorsata*. (white <1950, white with black point ≥1950 <2000, black ≥2000, ? = uncertain record, + datum unknown).

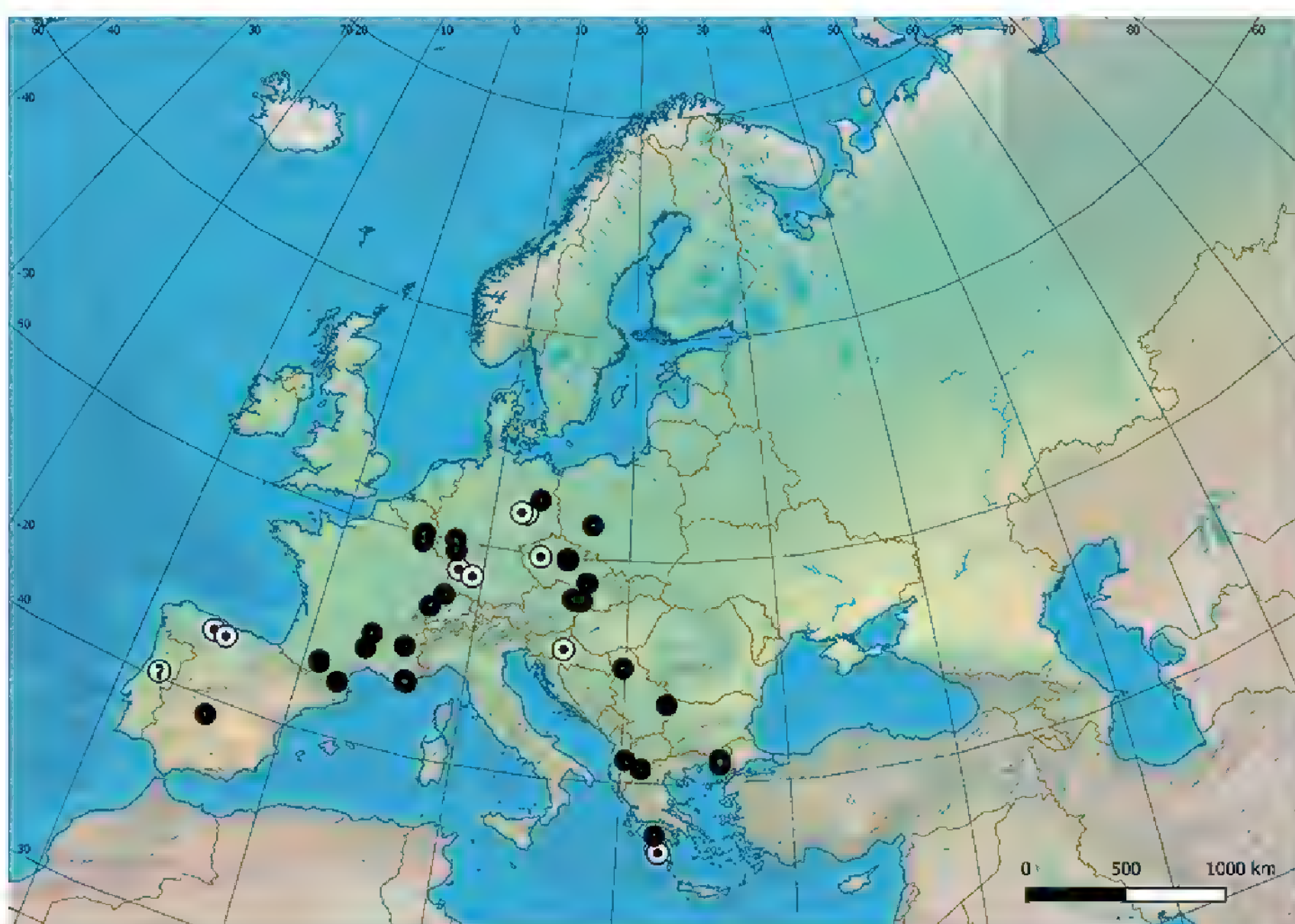


Fig. 26. Distribution map. *Brachyopa grunewaldensis*. (white <1950, white with black point ≥1950 <2000, black ≥2000, ? = uncertain record).

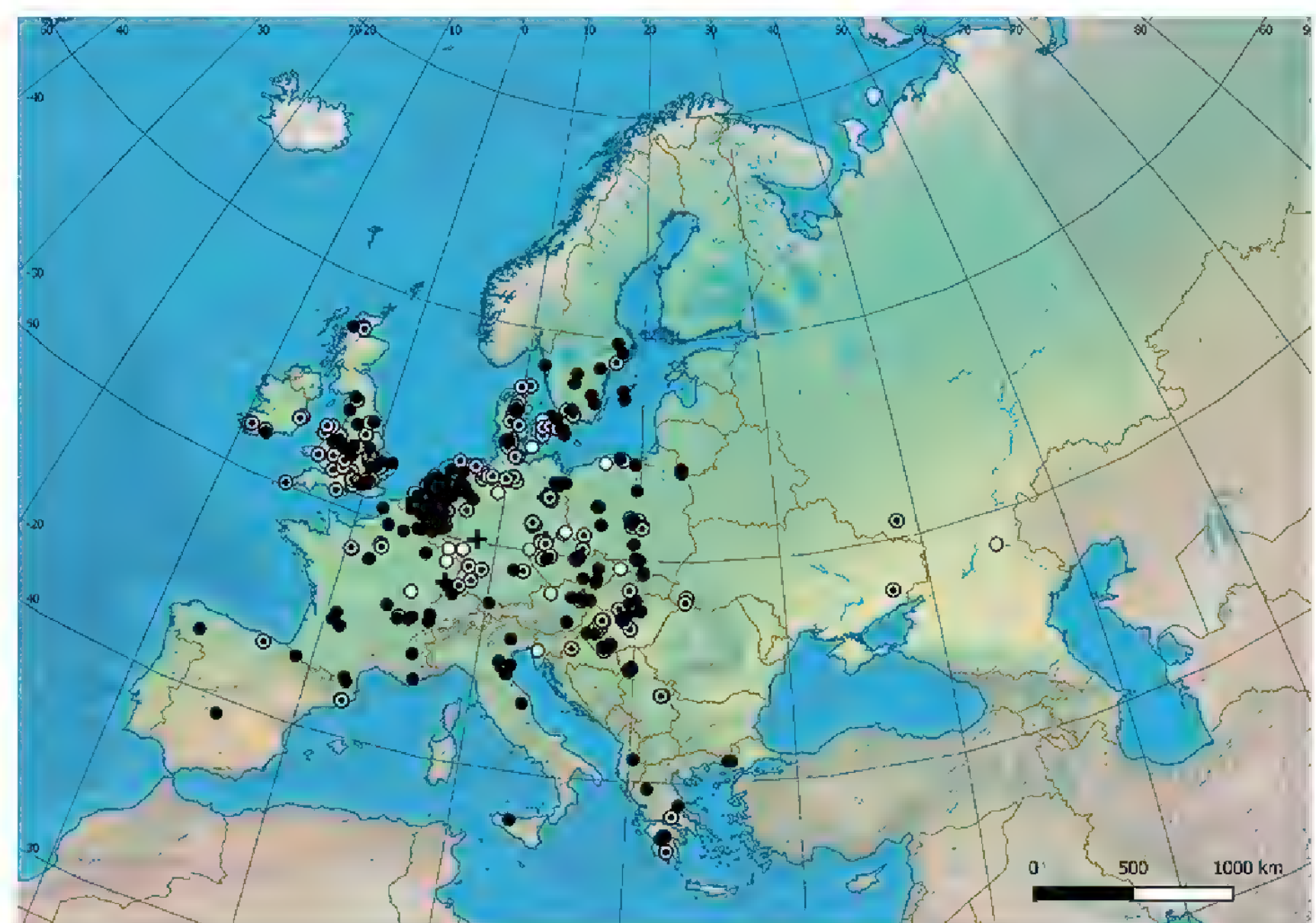


Fig. 27. Distribution map. *Brachyopa insensilis*. (white <1950, white with black point ≥1950 <2000, black ≥2000, + datum unknown).

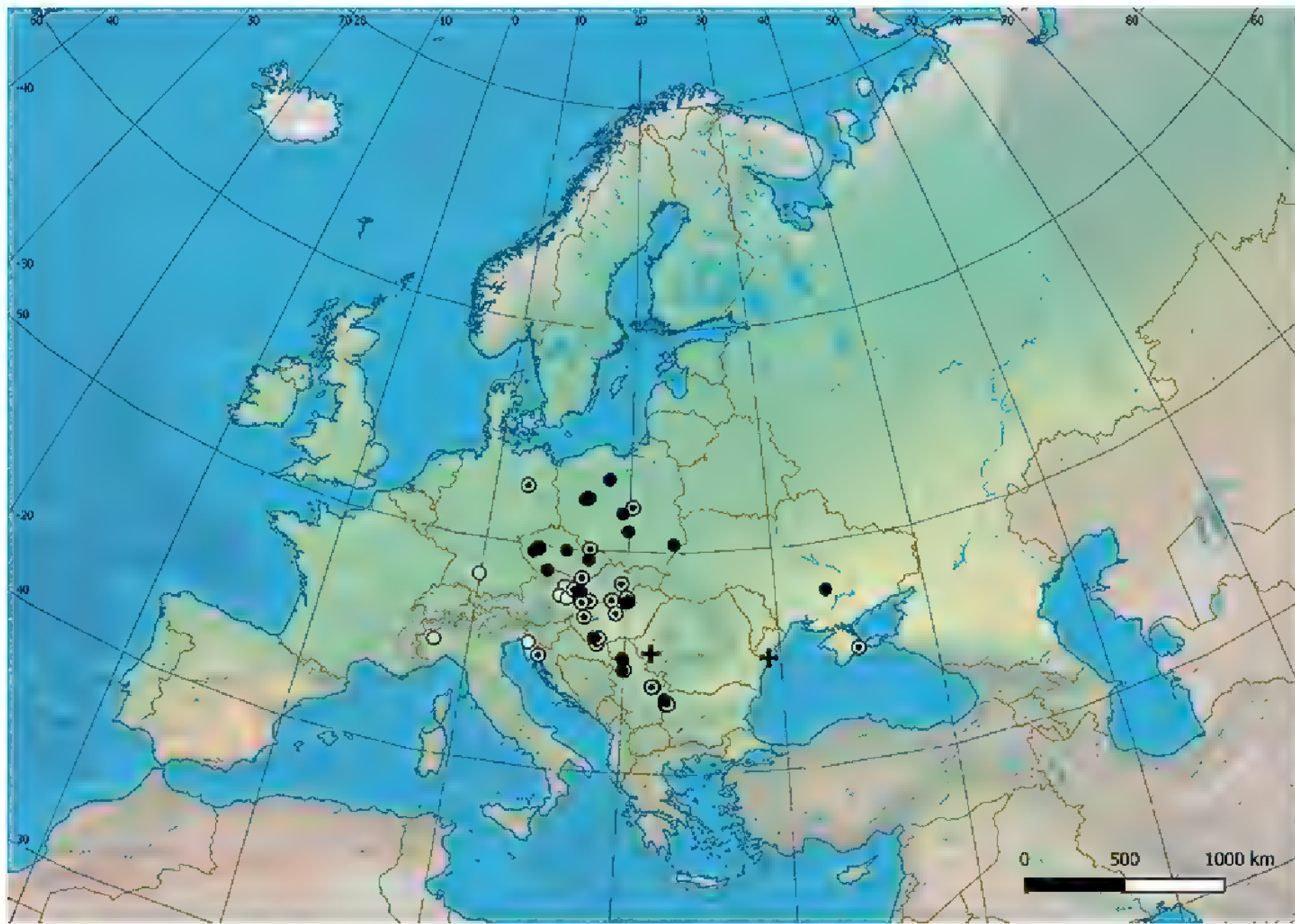


Fig. 28. Distribution map. *Brachyopa maculipennis*. (white <1950, white with black point ≥ 1950 <2000, black ≥ 2000 , + datum unknown).

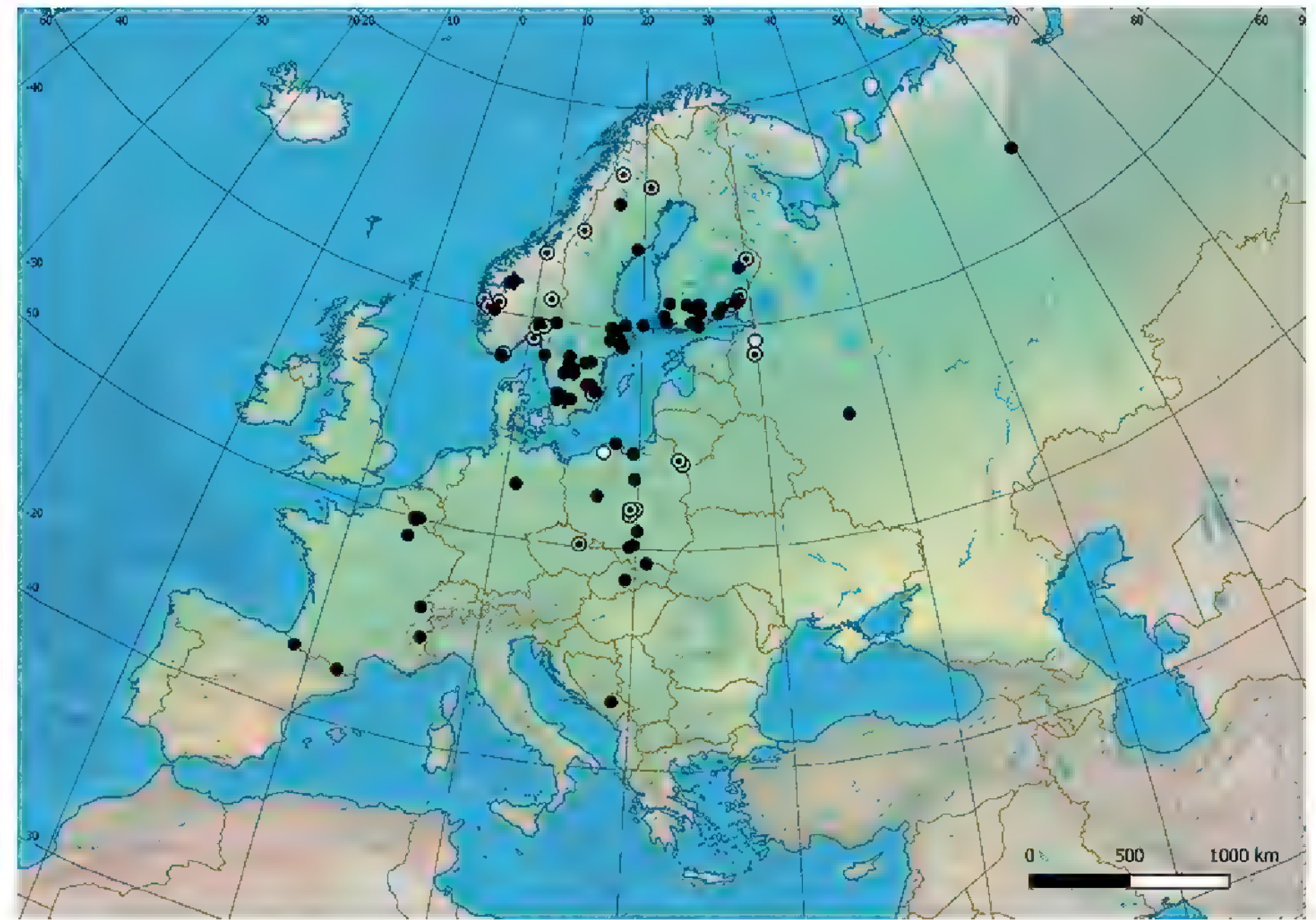


Fig. 29. Distribution map. *Brachyopa obscura*. (white <1950, white with black point ≥ 1950 <2000, black ≥ 2000).

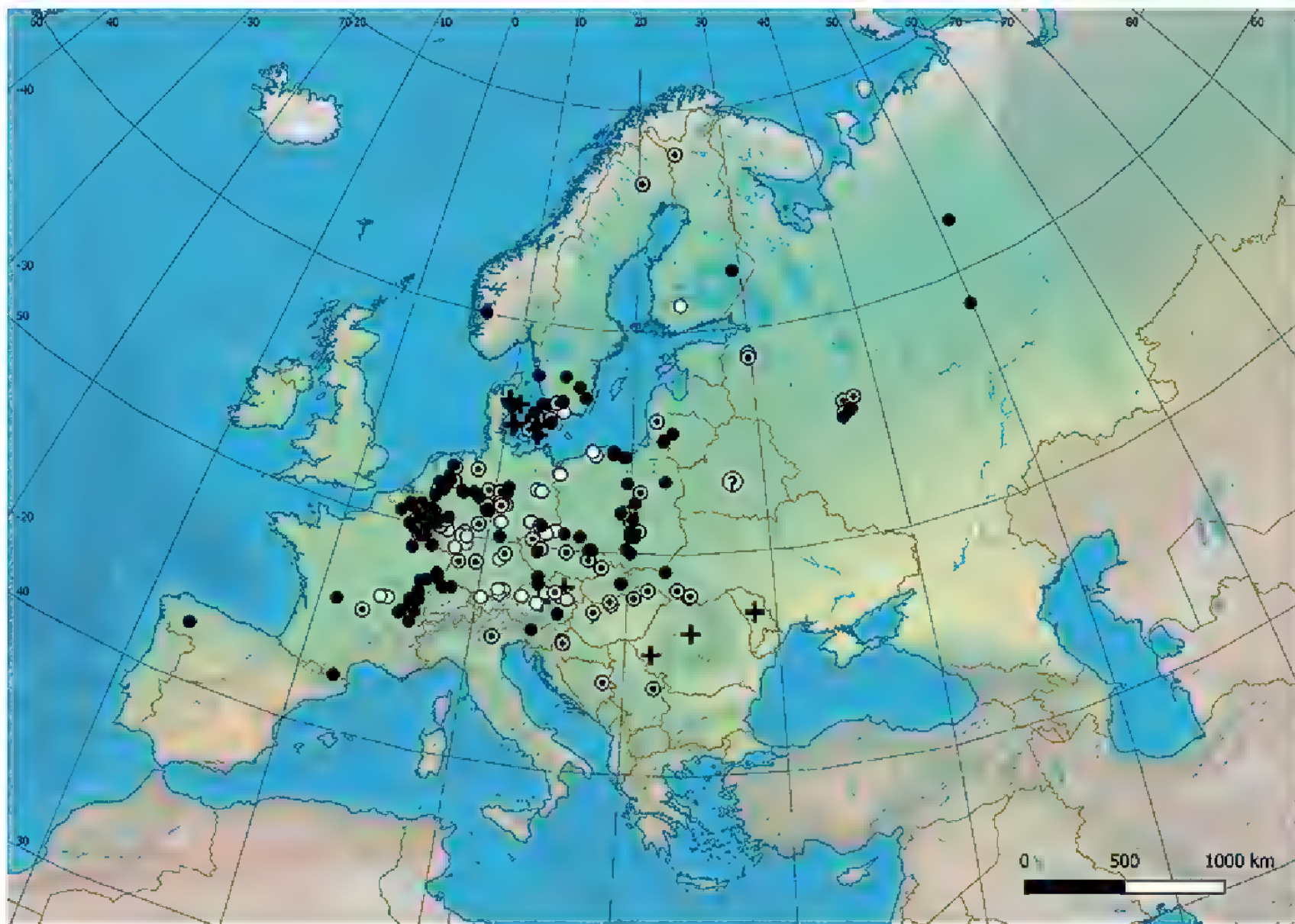


Fig. 30. Distribution map. *Brachyopa panzeri*. (white <1950, white with black point ≥ 1950 <2000, black ≥ 2000 , ? = uncertain record, + datum unknown).

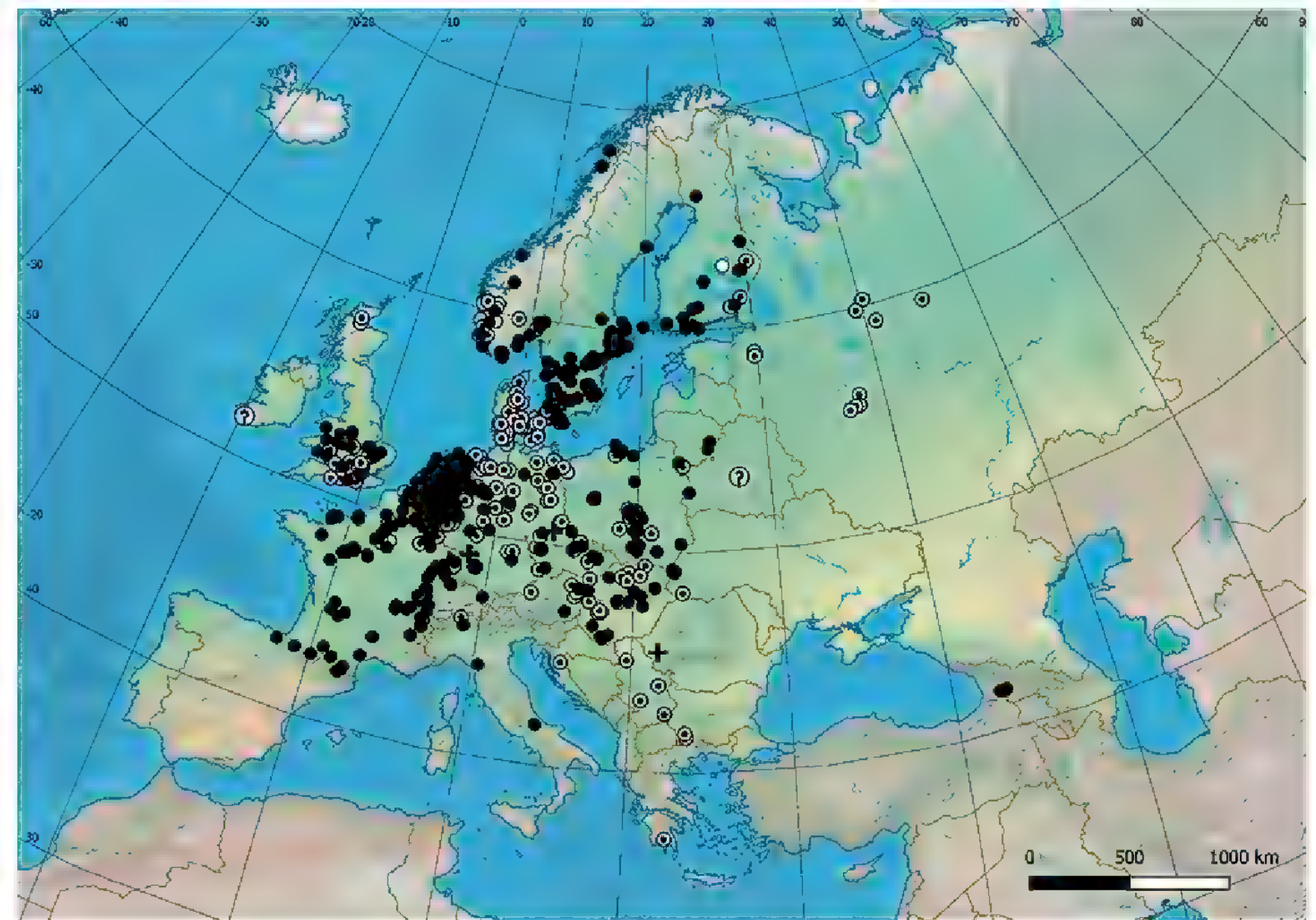


Fig. 31. Distribution map. *Brachyopa pilosa*. (white <1950, white with black point ≥ 1950 <2000, black ≥ 2000 , ? = uncertain record, + datum unknown).

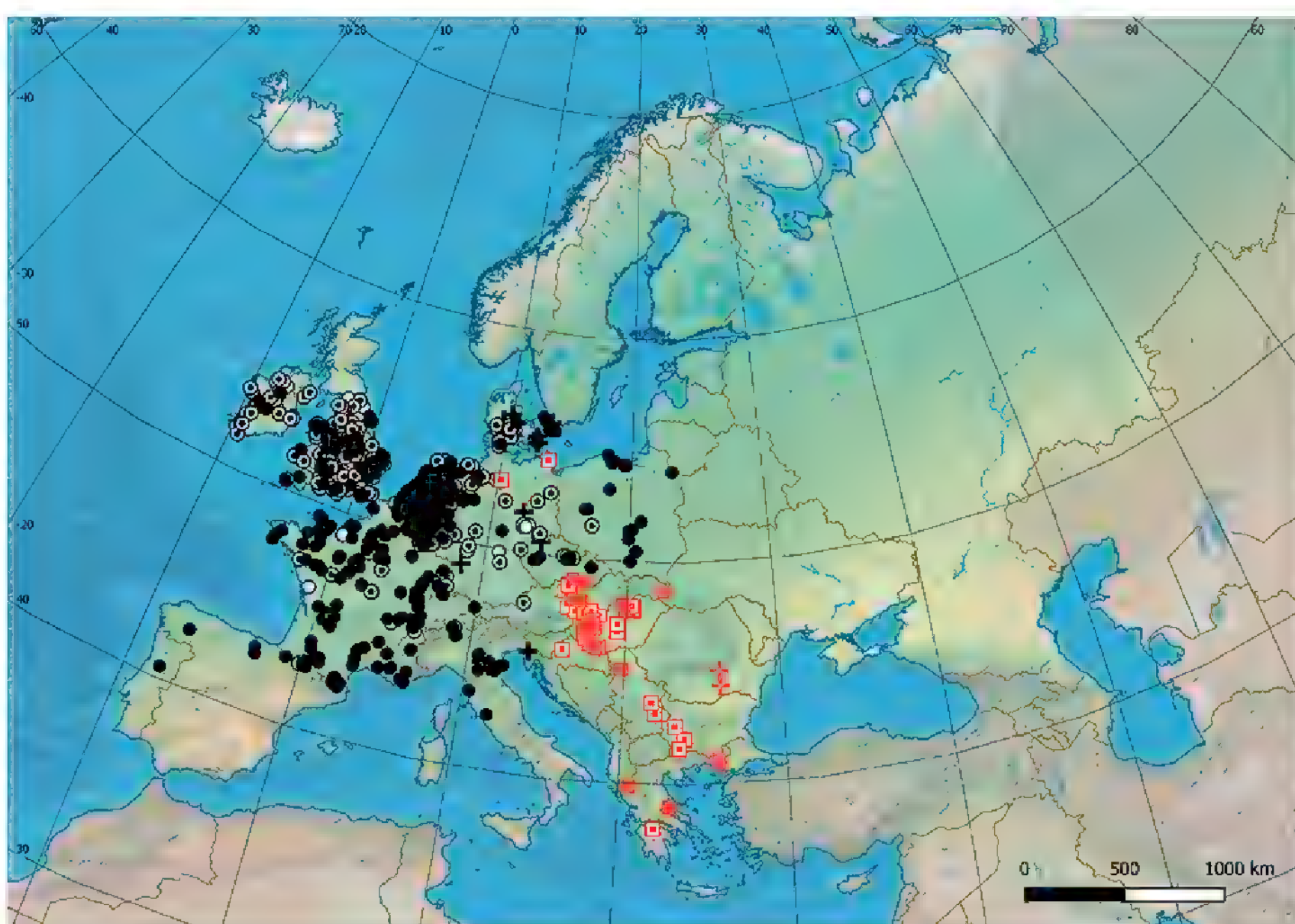


Fig. 32. Distribution map. *B. scutellaris*, black dot; *Brachyopa plena*, red square. (white <1950, white with black/red point ≥ 1950 <2000, black/red ≥ 2000 , + datum unknown).

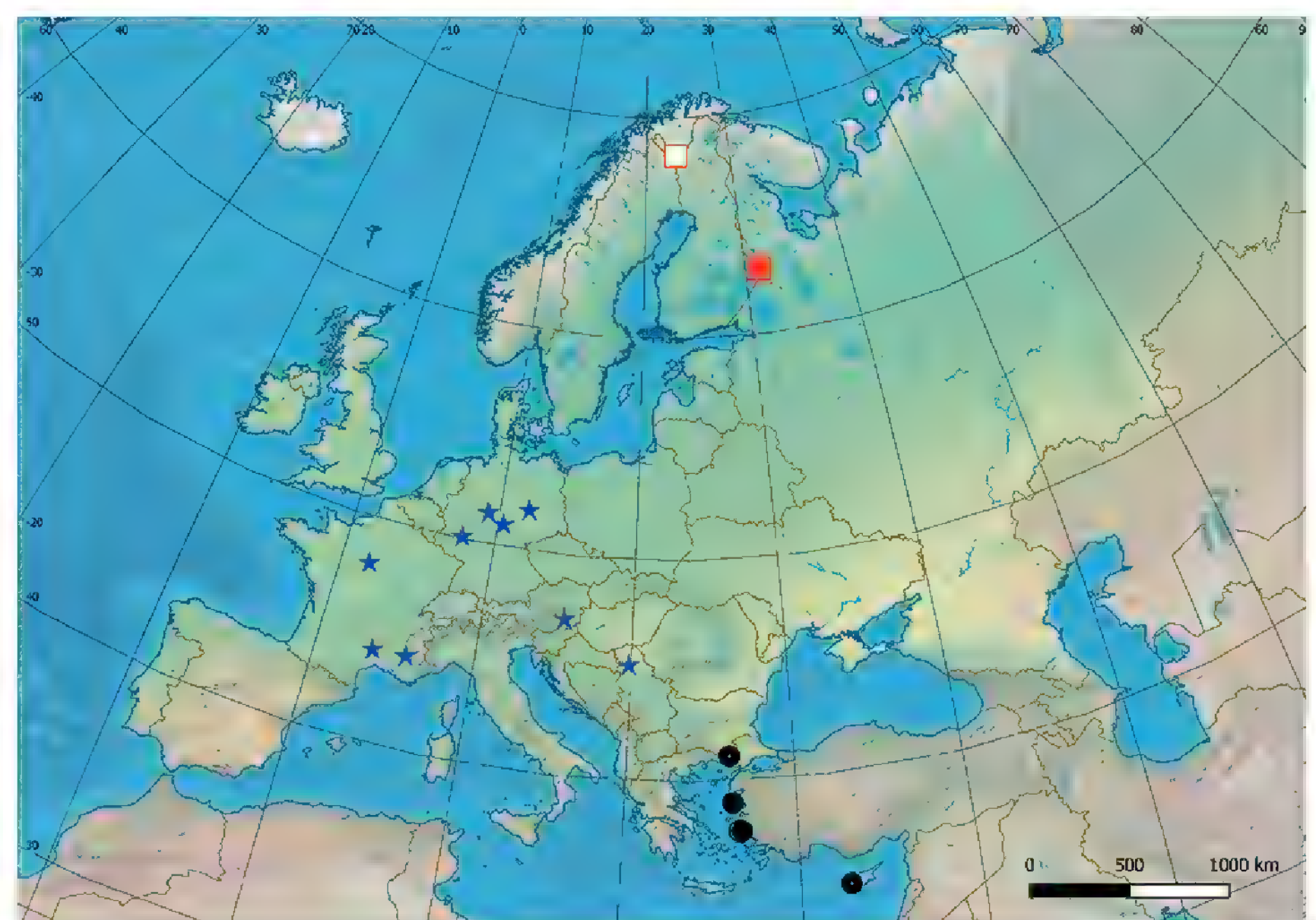


Fig. 33. Distribution map. *Brachyopa quadrimaculosa*, dot; *B. silviae*, stars; *B. zhelochovtsevi*, square. (white <1950, white with black point ≥ 1950 <2000, black ≥ 2000).

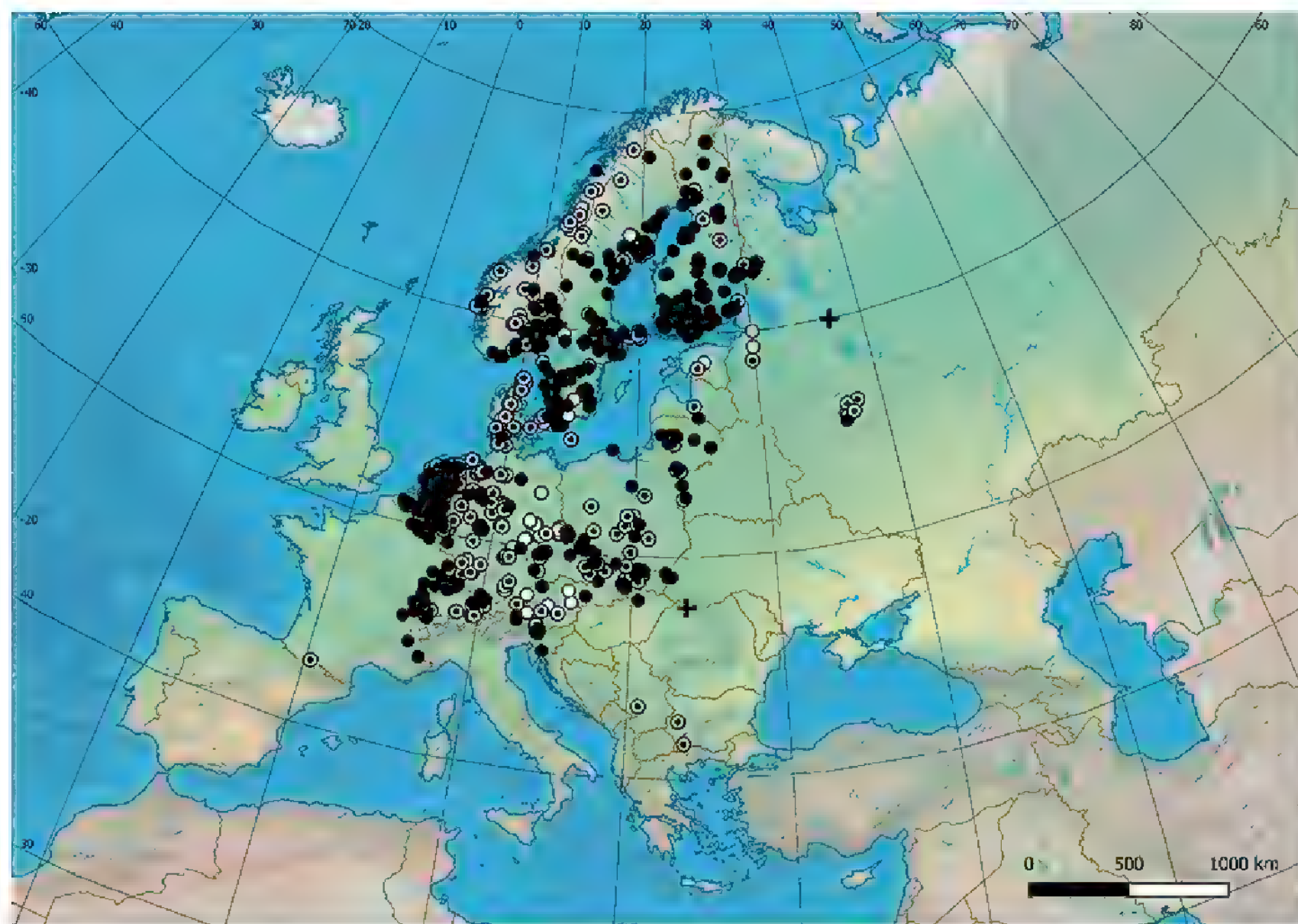


Fig. 34. Distribution map. *Brachyopa testacea*. (white <1950, white with black point ≥ 1950 <2000, black ≥ 2000 , + datum unknown).

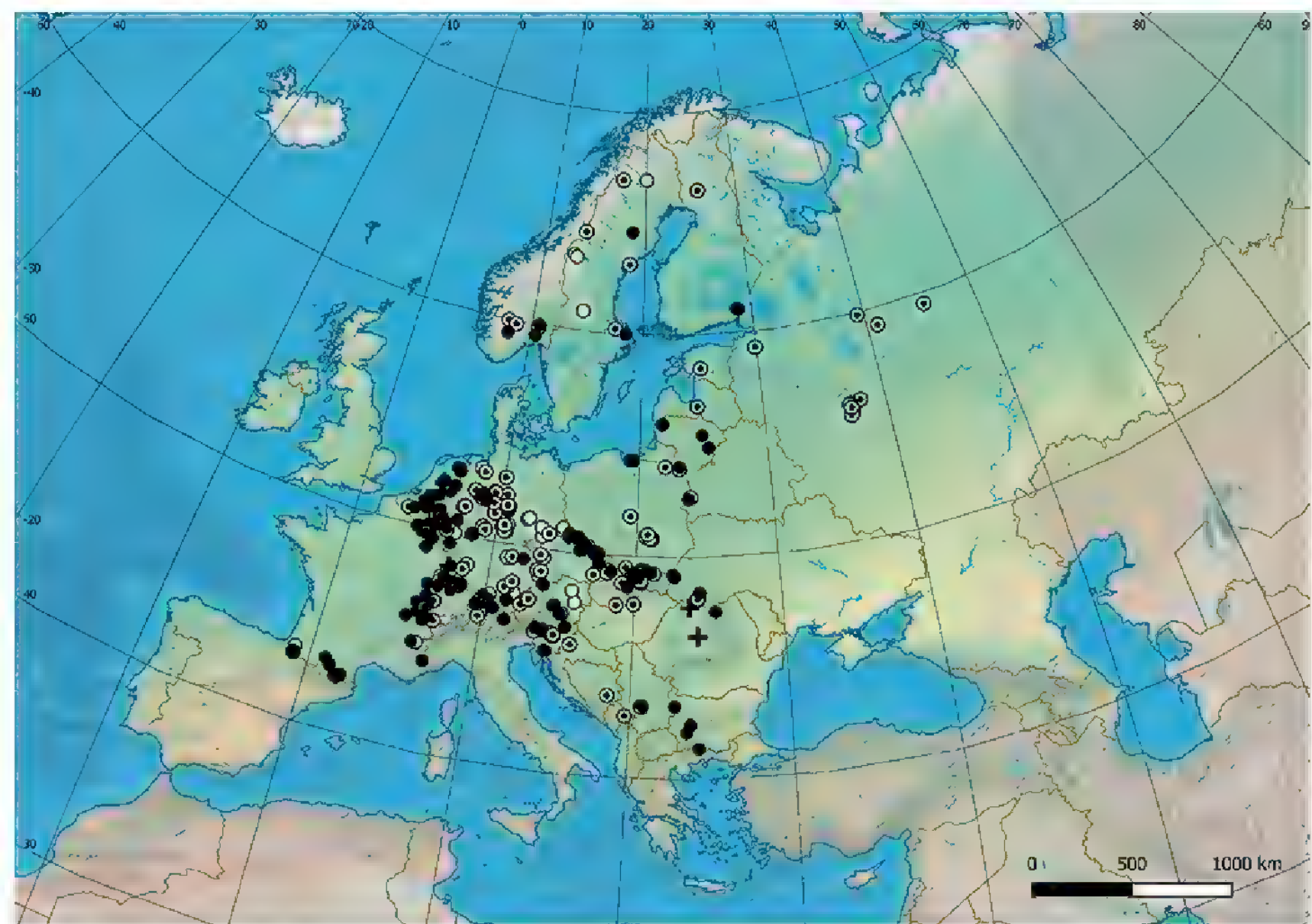


Fig. 35. Distribution map. *Brachyopa vittata*. (white <1950, white with black point ≥ 1950 <2000, black ≥ 2000 , + datum unknown).

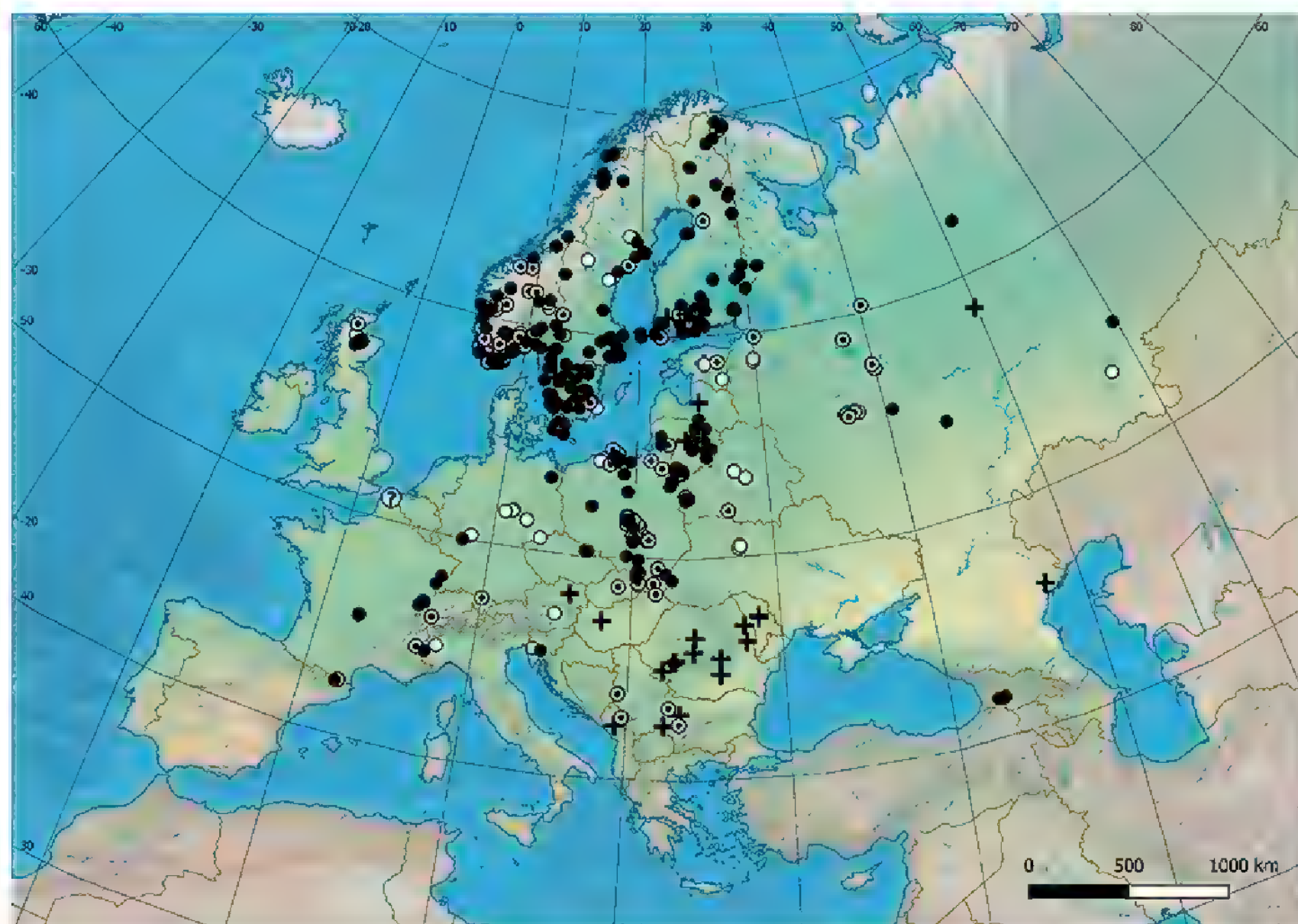


Fig. 36. Distribution map. *Hammerschmidtia ferruginea*. (white <1950, white with black point ≥ 1950 <2000, black ≥ 2000 , ? = uncertain record, + datum unknown).

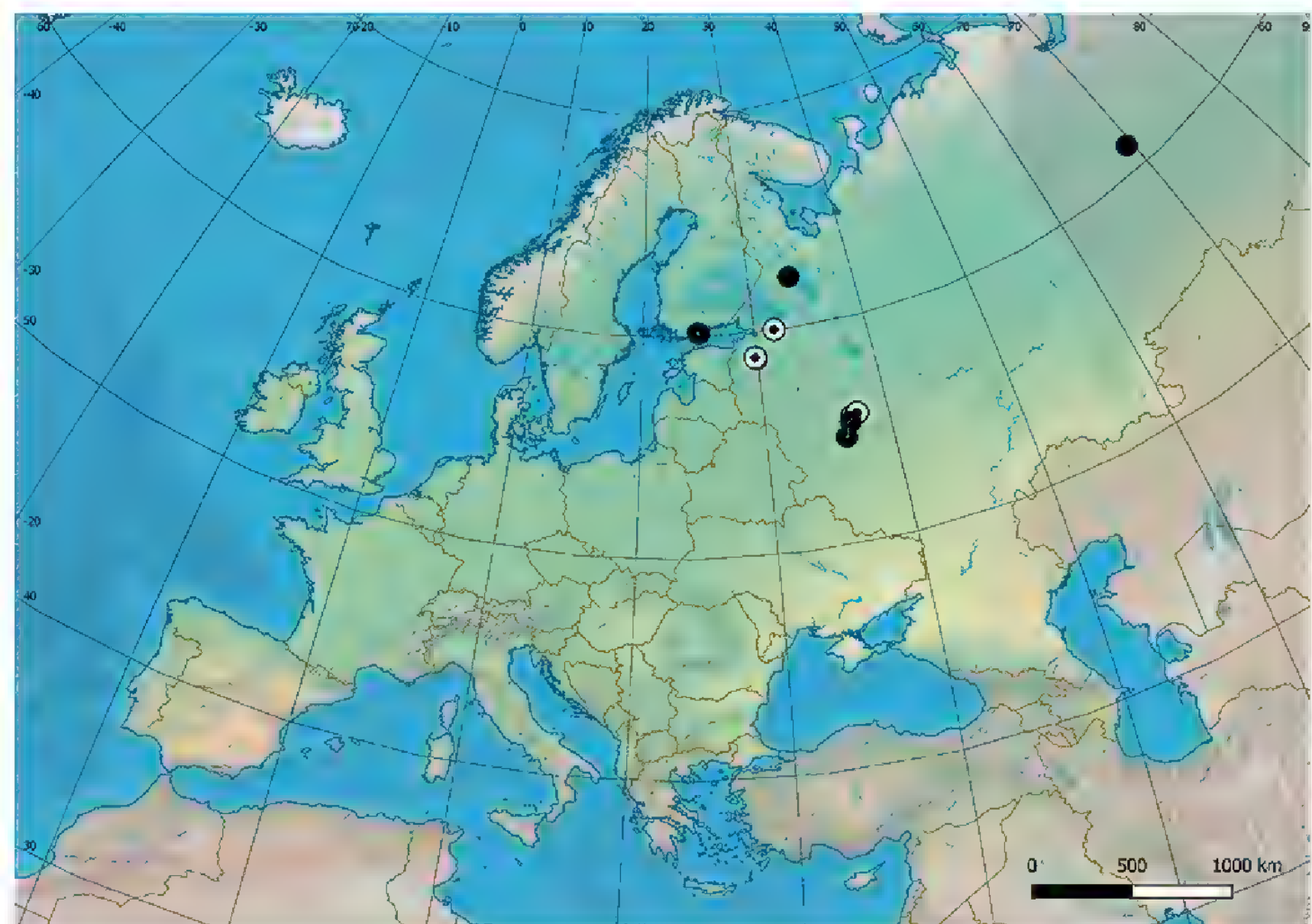


Fig. 37. Distribution map. *Hammerschmidtia ingraca*. (white <1950, white with black point ≥ 1950 <2000, black ≥ 2000).

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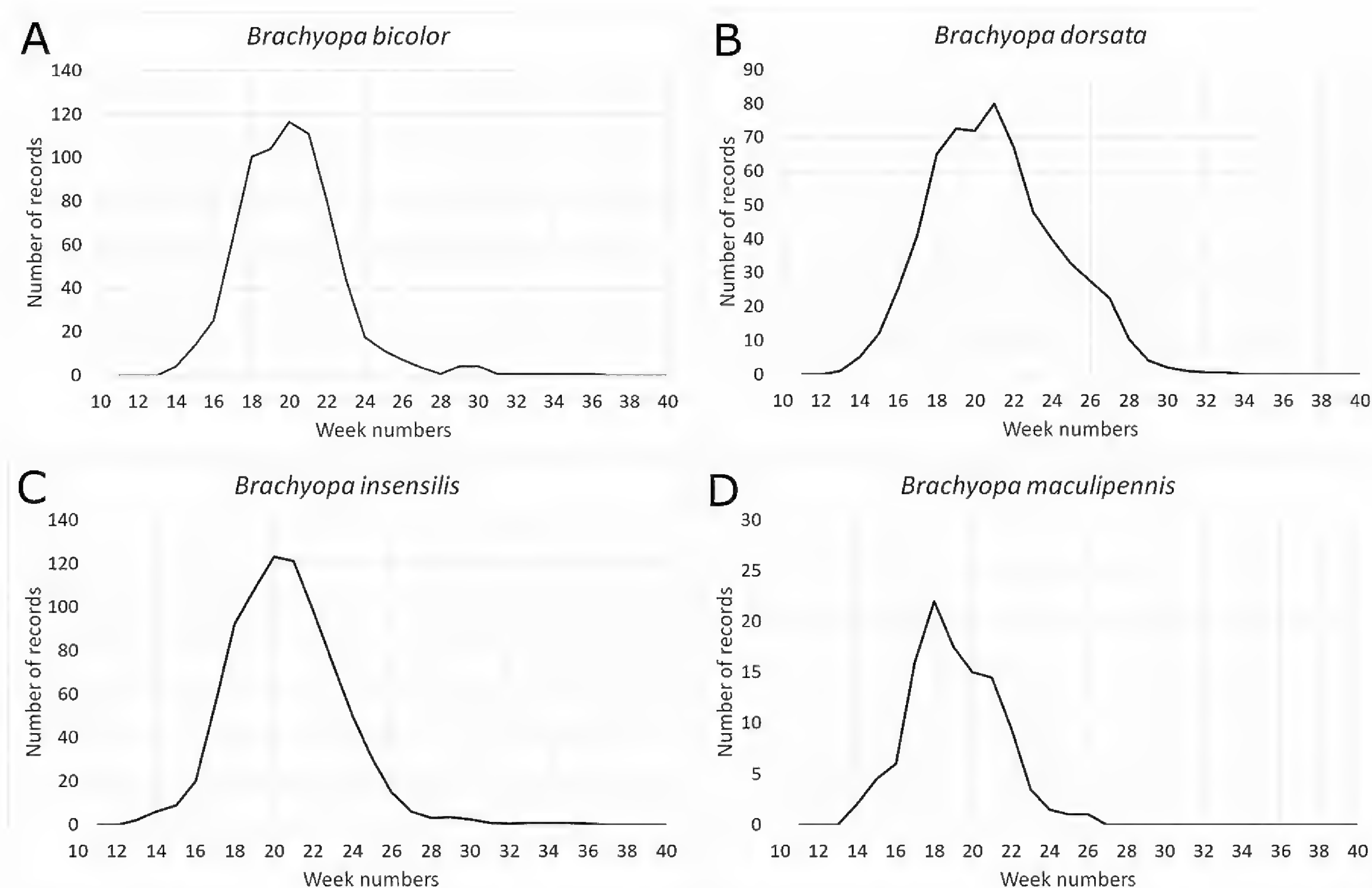


Fig. 38. Flight diagram. Moving average over 2 weeks with number of records of males and females in each calendar week. Week 10 beginning of March and week 40 end of September. **A.** *Brachyopa bicolor*. **B.** *Brachyopa dorsata*. **C.** *Brachyopa insensilis*. **D.** *Brachyopa maculipennis*.

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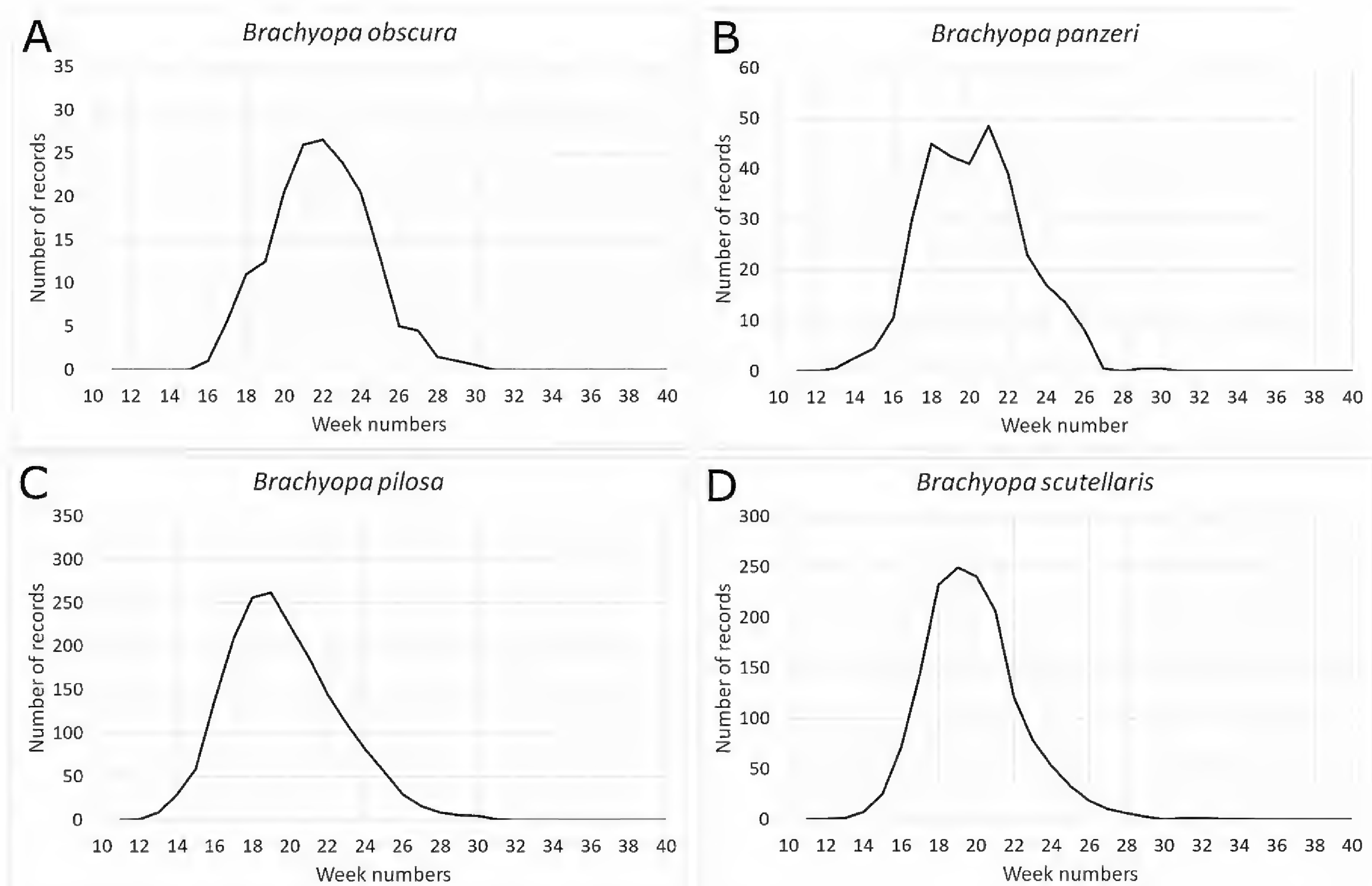


Fig. 39. Flight diagram. Moving average over 2 weeks with number of records of males and females in each calendar week. Week 10 beginning of March and week 40 end of September. **A.** *Brachyopa obscura*. **B.** *Brachyopa panzeri*. **C.** *Brachyopa pilosa*. **D.** *Brachyopa scutellaris*.

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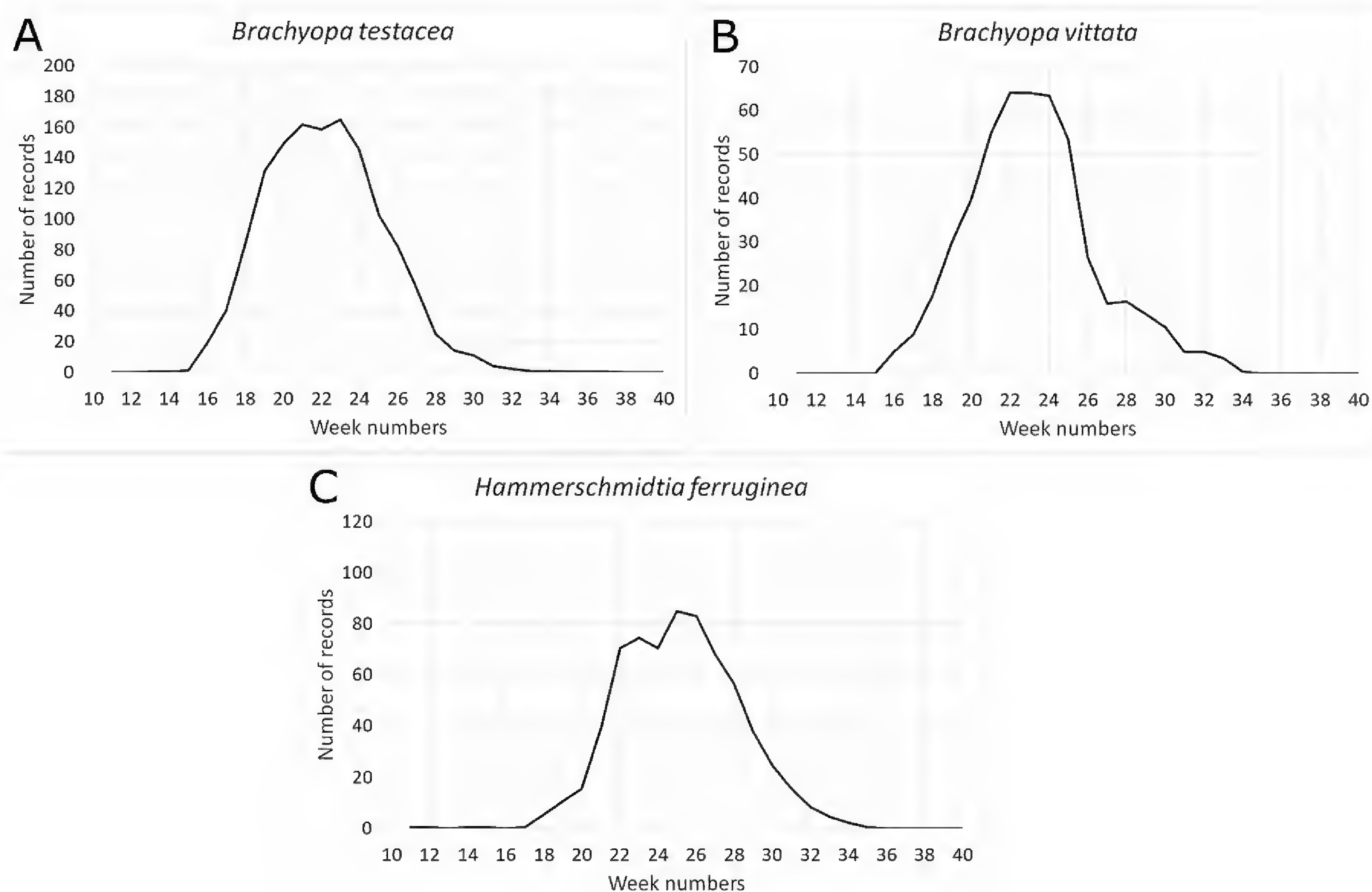


Fig. 40. Flight diagram. Moving average over 2 weeks with number of records of males and females in each calendar week. Week 10 beginning of March and week 40 end of September. **A.** *Brachyopa testacea*. **B.** *Brachyopa vittata*. **C.** *Hammerschmidtia ferruginea*.

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The snakes of Chad: results of a field survey and annotated country-wide checklist

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Abstract. From 2015 to 2017 we sampled snakes in most regions of the Republic of Chad, Central Africa. A total of 1,512 snakes belonging to 66 species were collected. Based on a full account of this collection, supplemented with additional museum specimens and reliable literature reports, we present an annotated checklist of the 80 snake species currently known from Chad, including 28 species that we added to the snake fauna of this country: *Letheobia weidholzi*, *Myriopholis occipitalis*, *Tricheilostoma sundewalli*, *Crotaphopeltis hippocrepis*, *Dasypeltis sahelensis*, *Natriciteres olivacea*, *Platycephalus florulentus*, *Spalerosophis diadema cliffordi*, *Telescopus tripolitanus*, *Atractaspis dahomeyensis*, *Atractaspis micropholis*, *Aparallactus lunulatus nigrocollaris*, *Boaedon longilineatus*, *Boaedon parolineatus*, *Boaedon perisilvestris*, *Boaedon subflavus*, *Lycophidion aff. capense*, *Malpolon moileensis*, *Micrelaps vaillanti*, *Prosymna ambigua*, *Prosymna greigerti*, *Psammophis afroccidentalis*, *Psammophis elegans*, *Psammophis mossambicus*, *Psammophis sudanensis*, *Rhamphiophis rostratus*, *Naja savannula* and *Echis romani*. Collecting localities for all specimens are provided and some taxonomical and biogeographical issues are discussed.

Key words. Squamata, Ophidia, biogeography, country checklist, venomous snakes, Central Africa.

INTRODUCTION

The Republic of Chad is the fifth largest country in Africa with an area of 1,284,000 km² between latitudes 7°N–23°N and longitudes 13°E–23°E. The northern part of the country is Saharan (Fig. 1), the central part is Sahelian (Fig. 2), or Sudano-Sahelian (Fig. 3), and the southern part is Sudanese (Fig. 4) or Sudano-Congolese (Fig. 5). South of 14°N elevation ranges from 280 m to 500 m a.s.l. in most parts of the country where the only significant reliefs are those of the Guera in central Chad (1,613 m a.s.l.) and the Monts de Lam in the southwest (1,163 m a.s.l.). North of 14°N, the Ouaddai plateau ranges from 500 m to 1,300 m a.s.l., the Ennedi plateau culminates at 1,450 m a.s.l., and the Tibesti mountains (Fig. 6)

at 3,414 m a.s.l. (Brami 2012). In northern Chad, the Bodélé depression is the lowest area of the country with 165 m a.s.l. and was occupied by Lake MegaChad at the Holocene before drying up (Leblanc et al. 2006). Average annual rainfall reaches a maximum of 1,200 mm south of 8°N and decrease progressively along a South-North gradient with 500 mm at 12°N and less than 5 mm north of 18°N, except in the Tibesti mountains where locally it may exceed 50 mm (Dubief 1963, Mahé et al. 2012). The southern and central parts of the country have a rich hydrological system, including Lake Chad, the Chari, Ouham and Logone rivers, and numerous seasonal tributaries. Each year during the rainy season (June–October) large parts of the country south of 13°N are flooded.



Fig. 1. The Sahara desert at Ounianga Serir in northern Chad ($18^{\circ}55'N$, $20^{\circ}54'E$) where *Cerastes cerastes* was collected.

Little data is available on the snakes of Chad. Rousset & Villiers (1965) reported a list of two hundred snakes belonging to 30 species from Gounou-Gaya ($09^{\circ}37'N$ / $15^{\circ}30'E$) and Bongor ($10^{\circ}16'N$ / $15^{\circ}22'E$). Graber (1966) reported a collection of 460 specimens from Fort-Lamy, now N'Djamena ($12^{\circ}06'N$ / $15^{\circ}02'E$), and other localities in central and northern Chad. Trape (2015) reviewed the reptile fauna of northern Chad. Museum specimens from Chad were included in works on certain genera or species, in particular by Roux-Estève (1969, 1974), Broadley (1971), Guibé & Roux-Estève (1972), Hughes (1976, 1977, 1983, 1985), Broadley (1984), Schätti (1985), Trape & Roux-Estève (1990), Broadley & Hughes (1993, 2000), Jakobsen (1997), Rasmussen (1997a, 1997b, 2005a, 2005b), Hahn & Wallach (1998), Wüster & Broadley (2003), Schätti & McCarthy (2004), Trape & Mané (2006a), Trape et al. (2006, 2012, 2019), Crochet et al. (2008), Chirio et al. (2011), Broadley et al. (2014, 2018), Trape & Mediannikov (2016), and Wüster et al. (2018). Sindaco et al. (2013) provided square-degree distribution maps of Palearctic species distributed in northern Chad. Some unpublished working documents for national parks management include lists of snake species, but they are based on presumed

distribution maps (e.g., those of Chippaux 1999), not on specimens really collected or observed in national parks.

MATERIALS AND METHODS

In May 2015, the first author contacted the last author for a field survey of the snakes of Chad. The Chad Ministry of Health was interested by this initiative and decided to provide logistic support and funds for a full research programme on snakebites and the distribution of snake species in all administrative regions of the country. The Baïbokoum area was selected by the Ministry of Health for the first survey since it was known as the place with the highest incidence and mortality from snakebite in Chad. From September 2015 to December 2017 additional surveys were conducted in most regions of the country. Local people at villages were asked to collaborate with the study and a total of 40 study areas were involved in the collection of snakes (Table 1), some of them represented by a single village or study site, and some others by several neighbouring villages (up to 18 villages for Baïbokoum area). Four of these study areas were located between $07^{\circ}00'N$ and $09^{\circ}00'N$, nine between $09^{\circ}00'N$ and $11^{\circ}00'N$, 12 between $11^{\circ}00'N$ and $13^{\circ}00'N$, eight



Fig. 2. The Sahel near Lake Chad at the end of the rainy season (13°48'N, 15°46'E). *Psammophis sudanensis* was the most abundant species at this latitude as in most other Sahelian and Sudano-Sahelian areas of Chad. The other common species between 13°N and 14°N were *Psammophis rukwae*, *Eryx colubrinus*, *Atractaspis watsoni*, *Boaedon subflavus*, *Naja haje* and *Echis leucogaster*.

between 13°00'N and 15°00'N, and seven north of 15°00'N (Fig. 7), where average annual rainfall ranges approximatively from 1,300–1,100 mm, 1,100–800 mm, 800–400 mm, 400–200 mm, and 200–<5 mm, respectively (Mahé et al. 2012).

Most specimens were deposited at the Programme National de Lutte contre le Paludisme (PNLP) office in N'Djaména. Selected specimens were deposited at the Institut de Recherche pour le Développement (Dakar, Senegal; acronym: IRD) or donated to the Museum national d'Histoire naturelle (Paris, France; acronym: MNHN). Specimens were identified to species according to regional keys (Trape & Mané 2006a, Chirio & LeBreton 2007) and further taxonomic analysis. For recent changes in snake generic names, we usually followed those adopted in the reptile database by Uetz et al. (2020).

The first author also examined specimens from Chad of the MNHN collection, most of them collected either by Decorse along the Chari River in 1903–1904 (Chabanaud 1917), or by Roussel and Stauch in the 1960s. Most Roussel's specimens were collected at Gounou-Gaya, some others at Bongor (75 km north of Gounou-Gaya), but all were published then preserved in part in the

MNHN collection with Mayo-Kebbi as collecting locality, i.e., the name of the province where the two localities are located (Roussel & Villiers 1965). However, these authors also provided for each species the vernacular names of snakes, which differ between Gounou Gaya and Bongor, thus allowing in most cases to establish which species were collected in each locality.

RESULTS

We collected a total of 1,512 specimens belonging to 66 species. Fourteen other species occur in Chad, including nine species from previous collections preserved at MNHN in Paris and five species reported in the literature. Altogether, the total number of snake species currently known from Chad is 80. Coordinates of our collecting localities are listed in Table 1, and those from MNHN and literature are listed in Table 2.

Table 1. Collecting localities of snakes in Chad (our study).

N	Locality	Latitude	Longitude	Altitude	Ecoregion	N° of specimens	N° of species
1	Arningmalik	14°02'N	21°07'E	716 m	Sahel	10	4
2	Bahar	12°03'N	21°19'E	511 m	Sahelo-Sudanese	61	15
3	Baïbokoum	07°44'N	15°41'E	515 m	Sudano-Congolese	505	40
4	Balani	09°42'N	15°00'E	351 m	Sudanese	8	5
5	Bereguit (7 km N)	11°39'N	19°08'E	502 m	Sahelo-Sudanese	1	1
6	Birim	13°26'N	14°44'E	287 m	Sahel	13	5
7	Bitanda	08°34'N	15°59'E	417 m	Sudanese	42	15
8	Bitea	13°30'N	20°54'E	537 m	Sahel	78	13
9	Bon Amdaoud	10°41'N	19°28'E	478 m	Sudanese	114	20
10	Djarat Abounimir	11°01'N	20°00'E	423 m	Sudanese	188	11
11	Dourenge	13°54'N	21°00'E	615 m	Sahel	10	6
12	Ennedi NW	17°32'N	21°29'E	822 m	Sahara	1	1
13	Fada	17°11'N	21°35'E	565 m	Sahelian	2	1
14	Faya Largeau	17°55'N	19°06'E	242 m	Sahara	1	1
15	Fiengbac	09°51'N	15°04'E	325 m	Sudanese	10	7
16	Goulmounbass	10°19'N	15°19'E	324 m	Sudanese	75	12
17	Gouroungali	13°13'N	21°03'E	564 m	Sahel	3	3
18	Guirli	12°40'N	21°20'E	568 m	Sahel	9	6
19	Hileborno	11°55'N	21°28'E	505 m	Sahelo-Sudanese	11	7
20	Kadam Digas	11°53'N	18°52'E	541 m	Sahelo-Sudanese	62	10
21	Kiéké	10°33'N	19°49'E	413 m	Sudanese	25	9
22	Laobida	09°13'N	15°07'E	425 m	Sudanese	49	13
23	Léré	09°39'N	14°13'E	235 m	Sudanese	2	1
24	Mahargal	12°07'N	21°22'E	527 m	Sahelo-Sudanese	50	9
25	Mao	14°08'N	15°18'E	305 m	Sahel	6	3
26	Masarma	12°33'N	16°35'E	292 m	Sahel	31	7
27	Matafo 2	13°31'N	14°40'E	291 m	Sahel	8	3
28	Mataya	11°59'N	18°02'E	406 m	Sahelo-Sudanese	3	2
29	Moïssala	08°20'N	17°45'E	385 m	Sudano-Congolese	55	18
30	Mongo (13 km S)	12°04'N	18°45'E	460 m	Sahel	1	1
31	Moundou	08°33'N	16°04'E	404 m	Sudanese	12	9
32	N'Djaména (Farcha)	12°06'N	14°58'E	295 m	Sahel	4	1
33	N'Djaména (Gassi)	12°03'N	15°08'E	298 m	Sahel	9	4
34	Ouadi Haouach	16°08'N	21°07'E	502 m	Sahel	1	1
35	Ouadi Sofoya / Torboul	15°55'N	20°58'E	479 m	Sahel	2	1
36	Oum Chalouba	15°48'N	20°46'E	452 m	Sahel	2	2
37	Ounianga Serir	18°55'N	20°54'E	360 m	Sahara	1	1
38	Tarhacha	13°38'N	20°50'E	526 m	Sahel	2	1
39	Tikem	09°49'N	15°03'E	335 m	Sudanese	5	5
40	Zamagouin	09°32'N	14°57'E	380 m	Sudanese	37	15
Total						1,512	66

Family Typhlopidae, Gray 1845

Afrotyphlops lineolatus (Jan, 1864)
Material: no specimen collected.
Other specimens (coll. MNHN): Fort-Lamy (= N'Djaména) (2), Chari (2).

Literature records: Fort-Lamy, Chari (Roux-Estève 1974).
Afrotyphlops punctatus (Leach, 1819)
Material: 15 specimens.
Localities: Baïbokoum (9), Bitanda (1), Bon Amdaoud (3), Moundou (1), Zamagouin (1).



Fig. 3. The Sahelo-Sudanese savanna in eastern Chad (11°45'N / 21°10'E) near Bahar, Hileborno and Mahargal study villages. The most common species collected in this area were *Psammophis rukwae*, *Psammophis sudanensis*, *Crotaphopeltis hotamboeia*, *Echis leucogaster* and *Atractaspis watsoni*.

Other specimens (coll. MNHN): Fort-Lamy (4), Mayo-Kebbi (1).

Literature records: Gounou-Gaya (Roussel & Villiers 1965), Fort-Lamy, Bisneye (Graber 1966), Fort Lamy, Mayo-Kebbi (Roux-Estève 1974).

Letheobia weidholzi Wallach & Gemel, 2018

Material: 1 specimen.

Locality: Baïbokoum (1).

Remarks: The Baïbokoum specimen is the holotype of *Letheobia logonensis* Trape, 2019, which we now consider as a junior synonym of *L. weidholzi* which was published independently a few months earlier, based on a single old museum specimen from Garoua (Cameroon). Our specimen was collected in a field near the Logone River. A third known specimen of this species was collected at Yola, Adamawa, Nigeria. It was erroneously attributed to *Letheobia praeocularis* (Stejneger, 1894) by Rasmussen (1997a) and Wallach & Gemel (2018). Both specimens are new country records and extend the range of *Letheobia weidholzi* to Nigeria and Chad.

Family Leptotyphlopidae Stejneger, 1892

Myriopholis adleri (Hahn & Wallach, 1998)

Material: no specimen collected.

Other specimens (coll. MNHN): Bongor (3).

Literature records: Bongor (Hahn & Wallach 1998, Trape 2002).

Remark: Bongor is the type locality and easternmost record of this species distributed from Senegal to Chad (Trape 2002, Trape & Mané 2006a). It was reported in error from Birao in Central African Republic by Chirio & Ineich (2006) (Trape unpublished).

Myriopholis boueti (Chabanaud, 1917)

Material: 12 specimens collected.

Localities: Bahar (3), near Béréguet (1), Bitea (1), Bon Amdaoud (2), Guirli (1), Kiéké (1).

Other specimens (coll. MNHN): Maillao (1), N'Djaména (2).

Literature records: Maillao, N'Djaména (Hahn & Wallach 1998, as *Leptotyphlops narirostris boueti*).

Table 2. Coordinates of snake records from Chad (literature data). The asterisks indicate approximate entries.

Locality	Longitude	Latitude	Altitude	Ecoregion
Abéché	13°50'N	20°49'E	540 m	Sahel
Archei	16°54'N	21°46'E	580 m	Sahel
Ati	13°13'N	18°20'E	335 m	Sahel
Ati (35 km SW)	13°00'N	18°06'E	334 m	Sahel
Aozou	21°48'N	17°25'E	920 m	Sahara
Bachikélé	16°32'N	22°20'E	720 m	Sahel
Baguirmi (region)	11°N*	16°E*	330 m*	Sahel/Sudanese
Bahr-el-Ghazal	14°30'N*	17°00'E*	285 m	Sahel
Bardaï	21°20'N	17°01'E	1020 m	Sahara
Batha	13°30'N*	18°30'E*	340 m	Sahel
Bisneye	12°40'N	16°10'E	290 m	Sahel
Bol	13°28'N	14°44'E	285 m	Sahel
Bokoro	12°22'N	17°03'E	300 m	Sahel
Bongor	10°16'N	15°22'E	335 m	Sudanese
Chari (River)	09/11°N*	15/18°E*	290/370 m	Sahel/Sudanese
Dejemine Batha	13°30'N*	18°30'E*	340 m	Sahel
Djintilo	12°49'N	14°33'E	290 m	Sahel
Fada	17°11'N	21°35'N	565 m	Sahel
Faya Largeau	17°55'N	19°06'E	242 m	Sahara
Fitri (Lake)	12°50'N	17°30'E	285 m	Sahel
Fort-Archambault (= Sarh)	09°08'N	18°22'E	370 m	Sudanese
Fort-Lamy (=N'Djaména)	12°06'N	15°01'E	298 m	Sahel
Goré	07°55'N	16°38'E	430 m	Sudano-Congolese
Gounou-Gaya	09°37'N	15°30'E	345 m	Sudanese
Iro (Lake)	10°06'N	19°26'E	390 m	Sudanese
Koalem	09°49'N	17°42'E	355 m	Sudanese
Koboué	17°25'N	22°03'E	790 m	Sahara
Koskobo	09°29'N	19°15'E	382 m	Sudanese
Koudoubol	13°24'N	14°43'E	285 m	Sahel
Kumao	07°36'N	15°36'E	575 m	Sudano-Congolese
Maillao	11°35'N	15°16'E	300 m	Sahelo-Sudanese
Mao	14°08'N	15°18'E	305 m	Sahel
Mayo-Kebbi (region)	09/10°N	14/15°E	350 m*	Sudanese
Mboura	07°35'N	15°35'E	530 m	Sudano-Congolese
Melfi	11°03'N	17°55'E	405 m	Sudanese
N'Djaména	12°06'N	15°01'E	298 m	Sahel
Ngodem	11°25'N	15°04'E	305 m	Sudanese
Niellim	09°42'N	17°48'E	365 m	Sudanese
Ouadi Fama	15°22'N*	20°34'E*	435 m	Sahel
Ouadi Rimé	14°00'N	18°00'E	309 m	Sahel
Oued Basso	17°30'N*	22°22'E*	845 m	Sahara
Oum Chalouba	15°48'N	20°46'E	452 m	Sahel
Oum El Adam	17°12'N	21°12'E	490 m	Sahara
Sarh	09°08'N	18°22'E	370 m	Sudanese
Tirreno (well)	21°34'N	17°19'E	1650 m	Sahara
Torboul (vicinity of)	15°57'N	21°59'E	626 m	Sahel
Yambatchingsou	09°11'N	15°10'E	402 m	Sudanese
Yebbi-Bou	20°55'N	18°05'E	1385 m	Sahara
Zakouma	10°53'N	19°49'E	420 m	Sudanese



Fig. 4. The Sudan Savanna and Salamat River at Zakouma National Park during the dry season (10°50'N, 19°47'E). Three study villages (Djarat Abounimir, Bon Amdaoud and Kiéké) were located at the eastern, western and southern limits of the park, respectively, where 25 snake species were collected.

Myriopholis lanzai Broadley, Wade & Wallach, 2014

Material: no specimen collected.

Other specimens (coll. MNHN): Faya (1).

Literature records: Faya Largeau (Le Berre 1989, as *Leptotyphlops macrorhynchus*); Chad (Hahn & Wallach 1998, as *Leptotyphlops cairi*), Faya Largeau (Broadley et al. 2014, Trape 2015).

Myriopholis occipitalis (Trape & Chirio, 2019)

Material: 1 specimen collected.

Locality: Moïssala (1).

Literature record: Moïssala (Trape & Chirio 2018).

Remarks: The type locality of this recently described species is located in Central African Republic (Kouki, 07°09'N / 17°18'E), 150 km south of Moïssala (Trape & Chirio 2019).

Tricheilostoma sundewalli (Jan, 1861)

Material: 1 specimen collected.

Locality: Baïbokoum (1).

Other specimen (coll. MNHN): Gounou-Gaya (1)

Literature record: Gounou-Gaya (Roussel & Villiers 1965, as *Leptotyphlops bicolor*).

Remarks: First record for Chad. *T. bicolor*, erroneously reported from Chad by Roussel & Villiers (1965), seems restricted to West Africa with Nigeria as easternmost limit.

Family Boidae Gray, 1825

Eryx colubrinus (Linnaeus, 1758)

Material: 15 specimens collected.

Localities: Birim (2), Bitea (2), Doureng (3), Gouroungali (1), Guirli (4), Matafo 2 (1), Tarhacha (2).

Other specimen (coll. MNHN): Bol (1).

Literature records: Abéché, Bahr-el-Ghazal, Bisneye, Mao (Graber 1966), Bachikélé, Ouadi Rimé (Trape 2015).

Eryx muelleri (Boulenger, 1892)

Material: 9 specimens collected.

Localities: Masarma (9).

Other specimens: Mayo Kebbi (1, coll. MNHN), Ouadi Rimé (1, coll. IRD).



Fig. 5. The Sudano-Congolese savanna in southern Chad near Moïssala is strongly impacted by agricultural activities (08°05'N, 17°40'E). The most common snake species were *Psammophis mossambicus*, *Psammophis sudanensis*, *Naja nigricollis* and *Lyco-phidion semicinctum*.

Literature records: Gounou-Gaya, Bongor (Roussel & Villiers 1965), Fort-Lamy, Bahr-el-Ghazal (Graber 1966).

Remark: On 23 January 2003, the first author observed several dozens of dessicated *Eryx* specimens around a dried pool of the Ouadi Rimé (14°00'54"N, 18°00'12"E). Several specimens were attributed to *E. colubrinus* in the field and a voucher specimen is attributable to *E. muel-leri*.

Family Pythonidae Fitzinger, 1826

Python regius (Shaw, 1802)

Material: 6 specimens collected.

Localities: Baïbokoum (5), Laobida (1).

Literature records: Gounou-Gaya, Bongor (Roussel & Villiers 1965).

Python sebae (Gmelin, 1788)

Material: 7 specimens collected.

Localities: Bitea (2), Hileborno (1), Kadam Digas (2), Mataya (1), Zamagouin (1).

Other specimen (coll. MNHN): south of Abéché (1).

Literature records: Gounou-Gaya, Bongor (Roussel & Villiers 1965), Batha, Bokoro, Bol, Fort-Lamy, Nokou, Ouaddaï (Graber 1966), Lac Fitri (ORSTOM, unpublished), Lac Iro (Pairault 1994), Zakouma (Dejace 2002).

Family Colubridae Oppel, 1811

Crotaphopeltis degeni (Boulenger, 1906)

Material: 23 specimens collected.

Localities: Djarat Abounimir (7), Fiengbac (1), Goulmounbass (11), Kiéké (2), N'Djaména (1), Tikem (1).

Other specimen (coll. MNHN): Ngodem (3).

Literature record: Ngodem (Rasmussen 1997b).

Crotaphopeltis hippocrepis (Reinhardt, 1843)

Material: 14 specimens collected.

Localities: Baïbokoum (2), Bitanda (1), Djarat Abounimir (11).

Remark: First record for Chad (but appeared in error on maps of Chippaux [1999] and Chippaux & Jackson [2019]).

Crotaphopeltis hotamboeia (Laurenti, 1768)



Fig. 6. The Tibesti mountains near the Pic Toussidé (3315 m) in the background and the caldera of the Trou du natron in the foreground (20°57'N, 16°33'E). Snake species currently known from the Tibesti include *Echis leucogaster*, *Cerastes cerastes*, *Cerastes vipera*, *Psammophis aegyptius* and *Platycephalus saharicus*.

Material: 122 specimens collected.

Localities: Bahar (18), Baïbokoum (18), Bitanda (3), Bon Amdaoud (10), Djarat Abounimir (48), Goulmounbass (1), Hileborno (1), Kadam Digas (7), Kiéké (6), Laobida (2), Mahargal (3), Moïssala (2), Moundou (1), Zamagouin (1).

Other specimens (coll. MNHN): Baguirmi (1), Maillao (4).

Literature records: Gounou-Gaya (Roussel & Villiers 1965), Ati, Bisneye, Fort-Lamy (Graber 1966).

Dasypeltis confusa Trape & Mané, 2006

Material: 2 specimens collected.

Locality: Baïbokoum (2).

Other specimen (coll. MNHN): Mayo Kebbi (1).

Literature records: Gounou-Gaya (Roussel & Villiers 1965, as *Dasypeltis scabra scabra*), Mayo Kebbi (Bates 2013).

Dasypeltis gansi Trape & Mané, 2006

Material: 14 specimens collected.

Localities: Baïbokoum (8), Laobida (2), Moïssala (2), Zamagouin (2).

Other specimen (coll. MNHN): Koudoubol (1).

Literature record: Bol, Koudoubol (Bates & Ineich, 2012).

Dasypeltis sahelensis Trape & Mané, 2006

Material: 7 specimens collected.

Localities: Bon Amdaoud (1), Goulmounbass (1), Guirli (1), Kadam Digas (2), Mahargal (1), N'Djaména (1).

Other specimens (coll. MNHN): N'Djaména (2).

Literature record: Fort-Lamy (Graber 1966, as *Dasypeltis scabra*).

Remarks: First record for Chad. All previous records of this species were either from West Africa or Morocco (Trape & Mané 2006b, Trape et al. 2012). We also attribute to *D. sahelensis* the El Geneina specimen (Darfur, Sudan) attributed to *D. scabra* by Colley (1946).

Dispholidus aff. *typus* (Smith, 1829)

Material: 6 specimens collected.

Localities: Baïbokoum (5), Moïssala (1).

Literature record: Gounou-Gaya (Roussel & Villiers 1965).

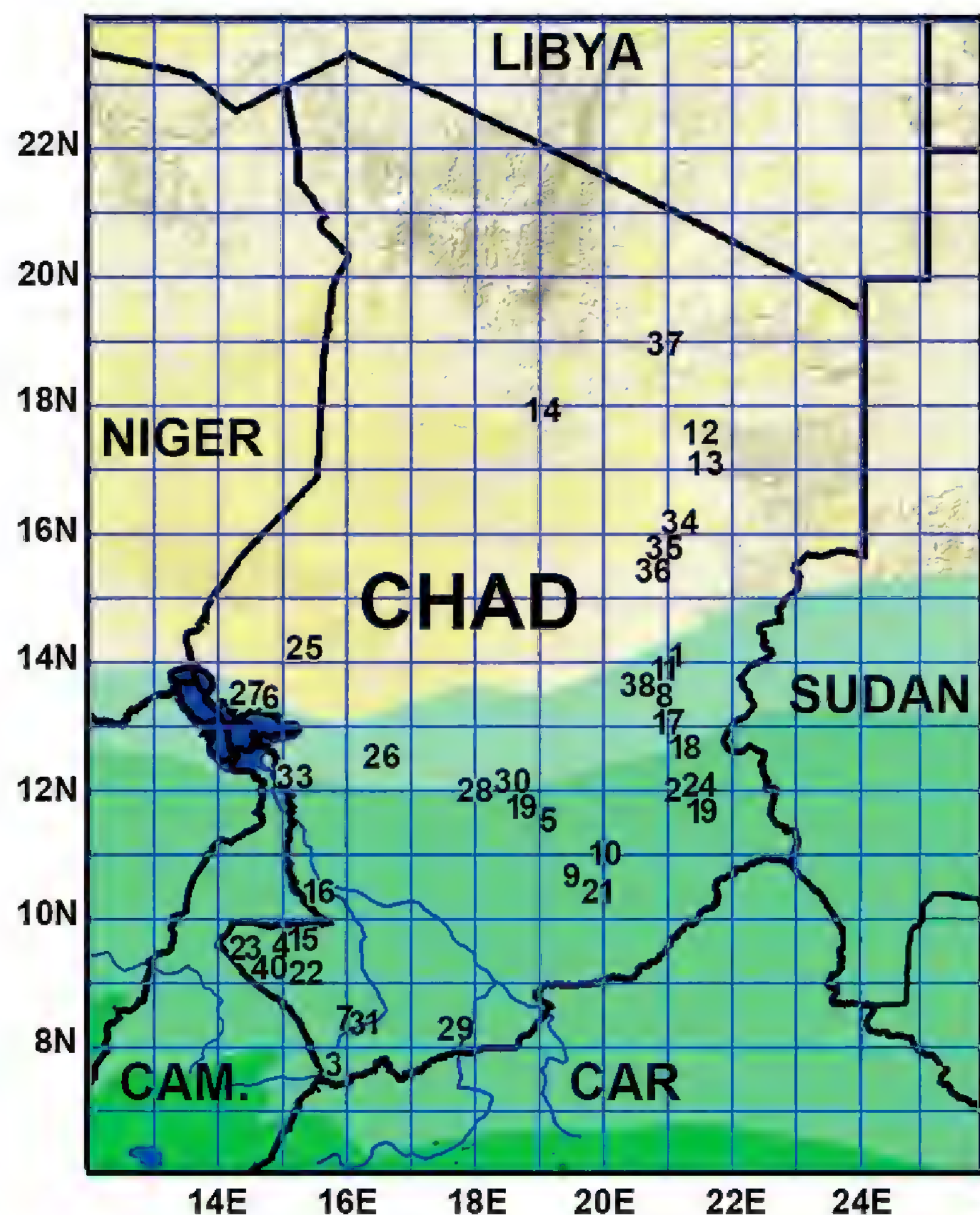


Fig. 7. Map of Chad with location of study areas. See Table 1 for locality numbers. Tikem and Balani, two close villages, and Farcha and Gassi, two suburbs of N'Djaména, are represented by a single number (4 and 33 respectively). Colours for vegetation areas: Congolese: dark green; Sudanese: green; Sahelian: light green; Saharan: yellow for sandy areas, white for stony areas, grey for rocky and mountainous areas.

Remarks: Molecular studies have shown that the Boomslang is a complex of several species, with *D. typus* restricted to southern South Africa (Eimermacher 2012). Perret (1961) highlighted some pattern and colour differences between the material he collected in Cameroon and the various subspecies described from D.R. Congo and Southern Africa. He proposed the name *occidentalis* ssp. n. for his material. Our specimens from Chad match the description of *occidentalis*.

Grayia smithii (Leach, 1818)

Material: no specimen collected.

Other specimens (coll. MNHN): Gounou-Gaya (1), Chari H656 (1).

Literature record: Gounou-Gaya (Roussel & Villiers 1965, as *Grayia tholloni*).

Remarks: The Gounou-Gaya specimen (MNHN 1965.397), previously attributed to *G. tholloni* by Roussel & Villiers (1965), is a male with only 15 rows of dorsal scales, 8(4) and 7(4) supralabials, 158 ventrals and 89 subcaudals. Despite its low number of dorsals, it clearly belongs to *G. smithii*. The Chari specimen (MNHN 1978.1832) has 7(4) supralabials on each side of the

head, 155 ventrals and a mutilated tail. It also presents a low number of dorsals, only 16 rows at midbody.

Meizodon coronatus (Schlegel, 1837)

Material: 4 specimens collected.

Localities: Baïbokoum (3), Laobida (1).

Literature record: Mayo-Kebbi (Roussel & Villiers 1965, Roux-Estève 1969).

Meizodon regularis Fisher, 1856

Material: no specimen collected.

Literature record: Koskobo (Schätti 1985).

Meizodon semiornatus tchadensis (Chabanaud, 1917)

Material: 1 specimen collected.

Localities: Bahar (1),

Other specimen (coll. MNHN): Koalem (1).

Literature records: Koalem (Chabanaud 1917, holotype of *Zamenis tchadensis*), Abéché, Fort-Lamy (Graber 1966, as *Meizodon coronatus*), Fort-Lamy (Roux-Estève 1969, Schätti 1985).

Natriciteres olivacea (Peters, 1854)

Material: 1 specimen collected.

Locality: Birim (1).

Other specimens (coll. MNHN): Maillao (2).

Remarks: First records for Chad and Lake Chad area.

Philothamnus bequaerti (Schmidt, 1923)

Material: 2 specimens collected.

Localities: Baïbokoum (1), Moïssala (1).

Literature record: Sarh (Hughes 1985).

Philothamnus hughesi Trape & Roux-Estève, 1990

Material: no specimens collected.

Other specimen (coll. MNHN): Chari (1).

Literature record: Chad (Trape & Roux-Estève 1990).

Remark: This specimen (MNHN 1904.0186) was collected by J. Decorse during the 1902–1904 Chari – Lake Chad expedition. There is no precise location but the most likely origin of this specimen is between 8°N and 9°N on the banks of the upper Chari River which is issued from the junction of Bamingui and Gribingui rivers. Additional specimens of *P. hughesi* were collected at the same latitude in Central African Republic (Chirio & Ineich 2006).

Philothamnus irregularis (Leach, 1819)

Material: 22 specimens collected.

Localities: Baïbokoum (18), Zamagouin (4).

Other specimen (coll. MNHN): Maillao (1).

Literature records: Gounou-Gaya (Roussel & Villiers 1965), Fort-Lamy (Graber 1966).

Philothamnus aff. *semivariiegatus* (Smith, 1840)

Material: 3 specimens collected.



Fig. 8. View of Baïbokoum area where 40 species of snakes were collected within only ten days. The Logone occidentale River is in the background, the rocky hill that dominates Baïbokoum is in the foreground (07°44'N, 15°40'E).

Localities: Baïbokoum (1), Moïssala (1), Moundou (1).

Other specimen (coll. MNHN): Maillao (1).

Remarks: *Philothamnus semivariatus* is now restricted to southern Africa (Engelbrecht 2019) and further molecular studies are needed to establish the status of Central African populations. This species complex is represented by *Philothamnus smithi* Bocage, 1882, in West Africa (Trape & Baldé 2014) and possibly also in Chad and the whole savannas areas north of the Congolese forest block.

Platyceps florulentus (Geoffroy, 1827)

Material: 6 specimens collected.

Localities: Arningmalik (1), Bitea (3), Doureng (2).

Remarks: First record for Chad. Our six specimens, all from Ouaddaï plateau, show 21 rows of dorsal scales, compared to 25 rows for the subspecies *P. f. perreti* (Schätti, 1988) from northern Cameroon and north-eastern Nigeria reliefs.

Platyceps saharicus Schätti & McCarthy, 2004

Material: No specimen collected.

Literature records: Aozou (Beck & Huard 1969, as *Zamenis rhodorachis*), Yebbi-Bou (Le Berre 1989, as *Coluber*

rhodorachis), Yebbi-Bou (Schätti & McCarthy 2004), Gouffre de Koboué (Geniez & Gauthier 2008), Aozou, Yebbi-Bou, Koboué (Trape 2015, as *Platyceps tessellata*).

Scaphiophis albopunctatus Peters, 1870

Material: 11 specimens collected.

Localities: Baïbokoum (6), Bon Amdaoud (2), Laobida (3).

Other specimens (coll. MNHN): Mayo-Kebbi (1), Maillao (1).

Literature records: Gounou-Gaya (Roussel & Villiers 1965), Fort-Lamy (Graber 1966), Maillao, Mayo-Kebbi (Broadley 1994).

Spalerosophis diadema cliffordi (Schlegel, 1837)

Material: no specimen collected.

Other specimen (coll. MNHN): Ouadi Fama (1).

Remark: First record for Chad.

Telescopus obtusus (Reuss, 1834)

Material: No specimen collected.

Literature record: Oum El Adam (Wake & Kluge 1961, as *Tarbophis obtusus*), Oum El Adam (Crochet et al. 2008, Trape 2015, as *Telescopus dhara obtusus*).

Telescopus tripolitanus (Werner, 1909)

Material: 12 specimens collected.

Localities: Bahar (1), Bitea (2), Bon Amdaoud (9).

Remark: First record for Chad.

Telescopus variegatus (Reinhardt, 1843)

Material: 14 specimens collected.

Localities: Baïbokoum (3), Laobida (9), Moïssala (1), Zamagouin (1).

Other specimen (coll. MNHN): Mayo-Kebbi (1).

Literature record: Gounou-Gaya (Roussel & Villiers 1965).

Family Lamprophiidae Ritzinger, 1843

Amblyodipsas unicolor (Reinhardt, 1843)

Material: 4 specimens collected.

Localities: Baïbokoum (2), Moïssala (1), Tikem (1).

Other specimen (coll. MNHN): Mayo-Kebbi (1).

Literature record: Gounou-Gaya (Roussel & Villiers 1965).

Aparallactus lunulatus nigrocollaris Chabanaud, 1916

Material: 4 specimens collected.

Locality: Baïbokoum (4).

Remark: First record for Chad.

Atractaspis aterrima Günther, 1863

Material: no specimen collected.

Other specimen (coll. MNHN): Fort-Archambaut (1).

Literature record: Chari (Rasmussen 2005a).

Atractaspis dahomeyensis Barboza du Bocage, 1887

Material: 4 specimens collected.

Locality: Baïbokoum (4).

Remarks: First record for Chad. This West African species seems to be very rare east of Nigeria where the only other records are those from Sternfeld (1908) in south-western Cameroon (Chirio & LeBreton 2007). *Atractaspis dahomeyensis* was erroneously reported from Central African Republic by Chippaux (1999) (plots on the distribution map are those of *A. watsoni*). Two of our Baïbokoum specimens were sequenced and proved similar to West African specimens (Portillo et al. 2019).

Atractaspis micropholis Günther, 1872

Material: 2 specimens collected.

Localities: Arningmalik (1), Gouroungali (1).

Remarks: First record for Chad. The occurrence of this species in Ouaddaï extends 900 km eastward the known distribution of this species previously reported from Senegal to Nigeria (Trape et al. 2006, Trape & Mané 2006).

Atractaspis watsoni Boulenger, 1908

Material: 56 specimens collected.

Localities: Bahar (3), Balani (2), Bitea (11), Bon Amdaoud (3), Djarat Abounimir (9), Goulmounbass (1), Guirli (1), Hileborno (3), Kadam Digas (14), Kiéké (1), Mahargal (2), Masarma (1), Zamagouin (5).

Other specimens (coll. MNHN): Mayo Kebbi (1), N'Djaména (2).

Literature records: Gounou-Gaya (Roussel & Villiers 1965, as *Atractaspis microlepidota*), Fort-Lamy (Graber 1966), Maillao, Mayo-Kebbi, N'Djaména (Trape et al. 2006).

Boaedon longilineatus Trape, 2016

Material: 18 specimens collected.

Localities: Bahar (1), Bon Amdaoud (2), Djarat Abounimir (6), Fiengbac (2), Goulmounbass (2), Hileborno (1), Masarma (3), Zamagouin (1).

Other specimens (coll. MNHN): Chari (2), Mayo-Kebbi (1).

Literature records: Gounou-Gaya (Roussel & Villiers 1965, as *B. fuliginosum* forme *lineatum*), Fort-Lamy (Graber 1966, as *B. fuliginosum* forme *lineatum*), Fiengbac, Goulmounbass, Zamagouin (Trape & Mediannikov 2016).

Remarks: This species recently described is currently known from Cameroon and Chad (Trape & Mediannikov 2016). We also attribute to *B. longilineatus* part of the specimens from El Geneina (Darfur, Sudan) attributed to *B. lineatus* by Colley (1946).

Boaedon parolineatus Trape & Mediannikov, 2016

Material: 34 specimens collected.

Localities: Baïbokoum (31), Bitanda (3).

Literature record: Baïbokoum (Trape & Mediannikov 2016).

Remark: This species recently described is currently known from Cameroon, Chad and Central African Republic (Trape & Mediannikov 2016, Trape unpublished).

Boaedon perisilvestris Trape & Mediannikov, 2016

Material: 2 specimens collected.

Locality: Baïbokoum (2).

Literature record: Baïbokoum (Trape & Mediannikov 2016).

Remark: This species recently described is currently known from Chad, Cameroon, SE Nigeria, Gabon, Congo-Brazzaville, D. R. Congo, Central African Republic and South Sudan (Trape & Mediannikov 2016, Nneji et al. 2019, Trape unpublished).

Boaedon subflavus Trape, 2016

Material: 125 specimens collected.

Localities: Bahar (8), Baïbokoum (60), Balani (2), Bitanda (5), Bitea (10), Bon Amdaoud (15), Doureng (1), Goulmounbass (1), Kadam Digas (9), Laobida (4), Mahargal (4), Moundou (3), Tikem (1), Zamagouin (2).

Literature record: Gounou-Gaya (Roussel & Villiers 1965, as *B. fuliginosum* “forme typique”), Fort-Lamy (Graber 1966, as *B. fuliginosum* “forme *fuliginosum*”), Baïbokoum, Balani, Goulmounbass, Kumao, Malgandi, Moundou, Tikem, Yambatchingsou, Zamagouin (Trape & Mediannikov 2016).

Remark: This species recently described is currently known from Cameroon, Central African Republic and Chad (Trape & Mediannikov 2016).

Gonionotophis grantii (Günther, 1863)

Material: 1 specimen collected.

Locality: Baïbokoum (1).

Literature record: a specimen of unknown origin is mapped near Bongor in Chippaux (2006) and Chippaux & Jackson (2019).

Hemirhagerhis nototaenia (Günther, 1864)

Material: 2 specimens collected.

Localities: Baïbokoum (1), Kiéké (1).

Other specimens (coll. MNHN): N'Djaména (1), Niellim (1).

Literature record: N'Djaména (Broadley & Hughes 2000).

Limaformosa crossi (Boulenger, 1895)

Material: 12 specimens collected.

Localities: Baïbokoum (10), Bitanda (1), Zamagouin (1).

Other specimen (coll. MNHN): Mayo-Kebbi (1).

Literature record: Gounou-Gaya (Roussel & Villiers 1965).

Remark: One specimen from Baïbokoum was included in the phylogeny and genus-level revision of the African file snakes *Gonionotophis* and *Mehelya* (Broadley et al. 2018).

Lycophidion aff. *capense* (Smith, 1831)

Material: 3 specimens collected.

Localities: Bon Amdaoud (2), Kiéké (1).

Remark: First record for Chad. Our specimens are three males with a single apical pit, a postnasal in contact with the first supralabial, 17-17-15 dorsals, 180-187 ventrals and 32-37 subcaudals. The top of the head and the snout are uniformly blackish, but there are limited white vermiculations on the side of the head. The dorsal scales have a light apical spot increasing in size on the lower lateral rows where they form a light border. The ventrum is uniformly dark except a light border on the more lateral part of the ventrals and white vermiculations on the throat. These specimens probably belong to an undescribed species since they differ from the nearest East-African representative of the *L. capense* complex (*L. capense jacksoni*) by a lower number of subcaudals and a different colour pattern (Broadley & Hughes 1993, Broadley 1996).

Lycophidion semicinatum (Duméril, Bibron & Duméril, 1854)

Material: 20 specimens collected.

Localities: Baïbokoum (8), Bitanda (3), Laobida (1), Moïssala (8).

Other specimens (coll. MNHN): Fort-Archambault (1), Mayo-Kebbi (1).

Literature records: Fort-Archambault, Mayo-Kebbi (Guibé & Roux-Estève 1972), Mayo-Kebbi (Roussel & Villiers 1965, as *Lycophidion irroratum*).

Lycophidion taylori Broadley & Hughes, 1993

Material: 2 specimens collected.

Localities: Bahar (1), Hileborno (1)

Other specimen (coll. MNHN): 20 km E of Abéché (1).

Literature record: Abéché (Broadley & Hughes 1993).

Malpolon moilensis (Reuss, 1834)

Material: 2 specimens collected.

Localities: Ennedi 17°32'N / 21°29'E (1), Ouadi Haouach (1).

Literature record: Ennedi 17°32'N / 21°29'E (Trape 2015, as *Rhagerhis moilensis*).

Remarks: The Ennedi specimen was the first record for Chad. We follow Figueroa et al. (2016) in reattributing this species to the genus *Malpolon*.

Micrelaps vaillanti (Mocquard, 1888)

Material: 7 specimens collected.

Localities: Bon Amdaoud (4), Kiéké (1), Mahargal (2).

Remarks: First record for Chad. The occurrence of this species in Sila and Salamat provinces, including the Zakouma National Park, extends 1,200 km westward the distribution of this species known from East Africa and Kurdufan in Sudan (Rasmussen 2002).

Prosymna ambigua Bocage, 1876

Material: 1 specimen collected.

Locality: Moïssala (1).

Remark: First record for Chad and northernmost record of these wet Congolese savanna species.

Prosymna collaris (Sternfeld, 1908)

Material: 10 specimens collected.

Localities: Bahar (4), Balani (2), Djarat Abounimir (1), Fiengbac (2), Moundou (1).

Other specimens (coll. MNHN): Mayo-Kebbi (3).

Literature records: Gounou-Gaya (Roussel & Villiers 1965, as *Prosymna meleagris*), Abéché, Fort-Lamy (Graber 1966, as *Prosymna meleagris*), Maillao, Mayo-Kebbi (Chirio et al. 2011, as *Prosymna greigerti collaris*).

Remarks: The occurrence of both *collaris* and *greigerti* patterns at Bahar (Sila province), Djarat Abounimir (Salamat province) and Moundou/Bitanda (Logone oriental province) support the view that these two taxa are best treated as separate species. As well documented in

other parts of West and Central Africa (Chirio et al. 2011) and confirmed in Chad, most of their respective ranges are distinct (mainly sahelian for *collaris* and sudanese for *greigerti*).

Prosymna greigerti Mocquard, 1906

Material: 17 specimens collected.

Localities: Bahar (4), Baïbokoum (4), Bitanda (1), Bon Amdaoud (1), Djarat Abounimir (15), Kadam Digas (3), Moïssala (1).

Remark: First record for Chad, all previous literature reports correspond to *P. collaris*.

Psammophis aegyptius Marx, 1958

Material: No specimen collected.

Other specimen (coll. MNHN): Dejemine Batha (1).

Literature records: Abéché, Bahr el Ghazal, Fort-Lamy (Graber 1966, as *Psammophis schokari*), puits de Tirenno (Beck & Huard 1969, as *Psammophis schokari*).

Psammophis afroccidentalis Trape, Böhme & Medianikov, 2019

Material: 1 specimen collected.

Locality: Mao (1).

Literature record: Mao (Trape et al. 2019).

Remarks: This specimen was included in the recent review and molecular study of the *Psammophis sibilans* group in Africa north of 12°S (Trape et al. 2019). It was the only specimen from Chad belonging to *Psammophis afroccidentalis*, a species new for Chad widely distributed in West Africa and previously confounded with *P. sibilans*. The specimens from other areas of Chad classically assigned to *P. sibilans* belong to *P. rukwae* or *P. sudanensis*.

Psammophis elegans elegans (Shaw, 1802)

Psammophis elegans univittatus Perret, 1961

Material: 16 specimens collected, including 14 *univittatus*.

Localities: Mao (2 *elegans*), Baïbokoum (6 *univittatus*), Bon Amdaoud (7 *univittatus*), Djarat Abounimir (1 *univittatus*).

Remarks: First record for Chad. Reported in error on maps of Chippaux (2006) and Chippaux & Jackson (2019). Interestingly Mao, north of Lake Chad, is the only known locality in Chad and the easternmost record for both *P. afroccidentalis* and the nominative subspecies of *P. elegans*.

Psammophis lineatus (Duméril, Bibron & Duméril, 1854)

Material: 64 specimens collected.

Localities: Baïbokoum (15), Bitanda (2), Goulmounbass (42), Léré (2), Zamagouin (3).

Other specimen (coll. MNHN): Mayo-Kebbi (1).

Literature record: Gounou-Gaya (Roussel & Villiers 1965, as *Dromophis lineatus*), Fort-Lamy (Graber 1966, as *Dromophis lineatus*).

Psammophis mossambicus (Peters, 1882)

Material: 61 specimens collected.

Localities: Baïbokoum (41), Bitanda (1), Laobida (6), Moïssala (12), Moundou (1).

Literature record: Fort-Archambault (Loveridge 1940, as *Psammophis sibilans phillipsii*).

Remarks: Several specimens were included in the recent review and molecular study of the *Psammophis sibilans* group in Africa north of 12°S (Trape et al. 2019). This study has shown that *P. phillipsii* is restricted to West Africa and that *P. mossambicus* is distributed both in southern Africa and north, east and south of the Congolese forest block.

Psammophis praeornatus gribinguiensis (Angel, 1921)

Material: No specimen collected.

Literature records: Logone region (Loveridge 1940, as *Dromophis praeornatus gribinguiensis*), Mayo-Kebbi (Roussel & Villiers 1965, as *Dromophis praeornatus*), Zakouma (Dejace 2002).

Psammophis rukwae Broadley, 1966

Material: 160 specimens.

Localities: Bahar (11), Baïbokoum (30), Birim (7), Bitea (7), Bon Amdaoud (3), Djarat Abounimir (37), Fiengbac (2), Goulmounbass (8), Gouroungali (1), Hileborno (2), Kadam Digas (5), Kiéké (10), Mahargal (11), Masarma (8), Matafo 2 (2), Mataya (2), N'Djaména Farcha (4), N'Djaména Gassi (5), Tikem (1), Zamagouin (4).

Literature records: Fort-Archambault (Loveridge 1940, as *Psammophis sibilans*), Gounou-Gaya (Roussel & Villiers 1965, as *Psammophis sibilans sibilans* forme typique), Fort-Lamy, Bokoro, Oum Chalouba (Graber 1966, as *Psammophis sibilans*, pro parte).

Remarks: Several specimens were included in the recent review and molecular study of the *Psammophis sibilans* group in Africa north of 12°S (Trape et al. 2019). *P. rukwae* ranges from East Africa to Chad and Cameroon and is replaced by *P. afroccidentalis* in West Africa, with *P. sibilans* restricted to Egypt, Sudan and Ethiopia.

Psammophis sudanensis Werner, 1919

Material: 174 specimens collected.

Localities: Arningmalick (4), Bahar (2), Baïbokoum (16), Balani (1), Bitea (30), Bon Amdaoud (25), Djarat Abounimir (45), Doureng (1), Goulmounbass (3), Guirli (1), Hileborno (2), Kadam Digas (13), Kiéké (2), Mahargal (15), Masarma (3), Moïssala (8), Moundou (1), Zamagouin (3).

Other specimens (coll. MNHN): Bol (1), N'Djaména (6).

Literature records: Gounou-Gaya (Roussel & Villiers 1965, as *Psammophis sibilans sibilans* pro parte), Fort-Lamy (Graber 1966, as *Psammophis sibilans* pro parte). Remarks: First record for Chad. Paradoxically, *P. sudanensis* is the most common snake in the Sahel and Sudan savannas of Chad. Almost all specimens have the lineated head and dorsal pattern typical of this species but some rare specimens are plain (e.g., IRD 2871.N from Arningmalick and IRD 2884.N from Bitea). Several specimens were included in the recent review and molecular study of the *Psammophis sibilans* group in Africa north of 12°S (Trape et al. 2019).

Rhamphiophis oxyrhynchus (Reinhardt, 1843)

Material: 55 specimens collected.

Localities: Bahar (1), Baïbokoum (21), Bitanda (11), Bon Amdaoud (8), Fiengbac (1), Goulmounbass (3), Kadam Digas (3), Laobida (3), Moïssala (2), Moundou (2).

Other specimens (coll. MNHN): Fort-Archambault (1), Maillao (1), Mayo-Kebbi (4).

Literature records: Gounou-Gaya (Roussel & Villiers 1965), Fort-Lamy (Graber 1966), Sarh (Chirio & Ineich 1991).

Rhamphiophis rostratus Peters, 1854

Material: 1 specimen collected.

Locality: Bitea (1).

Remarks: First record for Chad, extending 950 km westward the distribution of this species known from Kurdufan in Sudan, and also distributed in eastern and southern Africa.

Family Elapidae Boie, 1827

Elapsoidea laticincta (Werner, 1919)

Material: 2 specimens collected.

Locality: Baïbokoum (2).

Literature record: Goré (Jakobsen 1997).

Remarks: The holotype designated by Werner is a female from Kadugli (Sudan) with 150 ventrals, 13 subcaudals, 13 pale bands on the dorsum of body and tail. The head is pale with forward prolongation of first dark nuchal band onto frontal where it is forked (see picture of the holotype in Jakobsen [1997]). This species has been reported from Sudan, South Sudan, D.R. Congo, Central African Republic, Cameroon and Chad (Jakobsen 1997, Chirio & LeBreton 2007). According to Broadley (1971, 1998) and Jakobsen (1997) this species is possibly conspecific with *E. semiannulata moebiusi*. However, according to Jakobsen (1997) the two taxa can be distinguished on the basis of the number of ventral scales (*laticincta* 139–151 in males and 140–150 in females, *moebiusi* 151–167 in males and 148–161 in females) and the dorsal pattern (*laticincta* 8–17 pale bands, usually with white reticulate pattern, *moebiusi* 10–21 bands without reticulate pattern). Two specimens from Baïbokoum (one male and

one female with 150 ventrals) fall in the range of variation of *E. laticincta* and present head and dorsal patterns similar to those of the holotype of *E. laticincta*.

Elapsoidea semiannulata moebiusi (Werner, 1897)

Material: 16 specimens collected.

Localities: Baïbokoum (14), Moïssala (2).

Other specimens (MNHN): Fort Archambault (1), Mayo-Kebbi (2).

Literature records: Gounou-Gaya (Roussel & Villiers 1965, as *Elapsoidea decosteri moebiusi*), Fort-Archambault, Mayo-Kebbi (Broadley 1971, 1998).

Remarks: Males (n = 10) have 152–157 ventrals and the only female 153. The number of pale bands range from 10 to 14 (body only), and from 11 to 17 when tail is included. The head pattern of the youngest specimens is not different of those of the two specimens we attributed to *E. laticincta* and the holotype from Kadugli. Further studies are needed to clarify the status of populations attributed to these two taxa in Chad and neighbouring countries of Central Africa.

Naja haje (Linnaeus, 1758)

Material: 22 specimens collected.

Localities: Baïbokoum (3), Birim (2), Bitanda (2), Bitea (1), Bon Amdaoud (3), Doureng (1), Mao (3), Masarma (1), Matafo 2 (4), Moïssala (1), Moundou (1).

Literature records: Gounou-Gaya (Roussel & Villiers 1965), Abéché, Fort-Lamy (Graber 1966).

Naja nigricollis Reinhardt, 1843

Material: 27 specimens collected.

Localities: Baïbokoum (8), Bon Amdaoud (4), Fiengbac (1), Goulmounbass (1), Laobida (2), Moïssala (9), Zama-gouin (2).

Other specimens (MNHN): Fort-Lamy (1), Mayo-Kebbi (1).

Literature records: Gounou-Gaya (Roussel & Villiers 1965), Abéché, Fort-Lamy (Graber 1966).

Naja nubiae Wüster & Broadley, 2003

Material: no specimen collected.

Other specimens (MNHN): Nord du Mont Ennedi (1), Ouadi Basso (1).

Literature records: Archei, Ennedi, Oued Basso (Wüster & Broadley 2003, Trape 2015).

Naja savannula Broadley, Trape, Chirio & Wüster, 2018

Material: 1 specimen collected.

Locality: Mboursa near Baïbokoum (1).

Literature record: Mboursa (Wüster et al. 2018).

Remarks: First record for Chad and easternmost record for this West African savanna species (Wüster et al. 2018). A 218 cm long specimen collected on the roof of a hut located on the banks of the Mbéré River which separates Chad from Cameroon.

Naja subfulva Laurent, 1955

Material: 2 specimens collected.

Localities: Birim (1), Bitanda (1).

Other specimen (coll. MNHN): Djintilo (1).

Literature records: Fort-Archambault (Graber 1966, as *Naja melanoleuca*), Lac Tchad (Buffrénil 1992, as *Naja melanoleuca*).

Remarks: The Birim specimen, on the northern edge of Lake Chad near Bor, is the northernmost record for this species (see Wüster et al. 2018).

Family Viperidae Oppel, 1811

Bitis arietans (Merrem, 1820)

Material: 8 specimens collected and 2 specimens observed but non preserved.

Localities: Baïbokoum (3), Bitea (1), Bon Amdaoud (1), Matafo 2 (1), Moïssala (2).

Sight record: Ouadi Sofoya (A. S. Djiddi, unpublished).

Photographic record: near Torboul (A. S. Djiddi, unpublished).

Other specimens (coll. MNHN): Bol (1), Maillao (2), N'Djaména (1).

Literature records: Gounou-Gaya (Roussel & Villiers 1965), Abéché, Ati, Fort-Lamy (Graber 1966), Zakouma (Dejace 2002).

Causus maculatus (Hallowell, 1842)

Material: 18 specimens collected.

Localities: Baïbokoum (8), Bitanda (1), Bon Amdaoud (8), Laobida (1).

Other specimens (coll. MNHN): Fort-Archambault (1), Mayo-Kebbi (1), Niellim (4).

Literature records: Gounou-Gaya (Roussel & Villiers 1965), Chari, Mayo-Kebbi, Melfi, N'Djaména, Sarh (Hughes 1977), see also square degree map of Rasmussen (2005b).

Causus resimus (Peters, 1862)

Material: 28 specimens collected.

Localities: Bahar (2), Bon Amdaoud (1), Djarat Abounimir (20), Mahargal (2), N'Djaména Gassi (2), Tikem (1). Other specimens (coll. MNHN): Bol (2), Chari (1), Mayo-Kebbi (3), Maillao (10), N'Djaména (13), Niellim (4).

Literature records: Mayo Kebbi (Roussel & Villiers 1965), Abéché, Ati, Fort-Foureaux, Fort-Lamy (Graber 1966, as *Causus rhombeatus*), Chari, Mayo-Kebbi, N'Djaména (Hughes 1977), see also square degree map of Rasmussen (2005b).

Cerastes cerastes (Linnaeus, 1758)

Material: 3 specimens collected.

Localities: Faya Largeau (1), Ounianga Serir (1), Oum Chalouba (1).

Literature records: Aozou, Yebbi-Bou (Pellegrin 1935), Ennedi, Bahr-el-Ghazal (Graber 1966), Aozou, Yebbi-Bou, Fada (Trape 2015).

Cerastes vipera (Linnaeus, 1758)

Material: no specimen collected.

Literature records: Tibesti (Graber 1966), Fada (Trape 2015).

Echis leucogaster Roman, 1972

Material: 40 specimens collected.

Localities: Arningmalik (4), Bahar (2), Bitea (7), Dou-reng (2), Fada (2), Guirli (1), Kadam Digas (4), Mahargal (10), Masarma (6), Mongo (1), Oum Chalouba (1).

Other specimens: Fada (1, coll. MNHN), 35 km SW of Ati (1, coll. IRD).

Literature records: Abéché, Ouaddai, Bahr-el-Ghazal, Bisneye, Zaghawa (Graber 1966, as *Echis carinatus*), between Bardaï and Aozou (Beck & Huard 1969, as *Echis carinata*), between Bardaï and Aozou, Fada (Trape 2015).

Remarks: Most specimens have a clear uniform venter, but some specimens with a spotted venter, at least on each side of the ventrals, were collected in southeastern Chad (6 of 13 specimens from Bahar, Guirli and Mahargal). Meristic data were similar to those of unspotted specimens. In West Africa, specimens of *E. leucogaster* with a spotted venter are not rare in western Mali and central Senegal (Trape & Mané 2017). Pending for comprehensive molecular studies including all the various taxa and populations of the *Echis pyramidum* complex in Africa we prefer to keep binomials for *E. leucogaster*.

Echis romani Trape 2018

Material: 155 specimens collected.

Localities: Baïbokoum (127), Bitanda (6), Fiengbac (1), Goulmounbass (1), Laobida (14), Zamagouin (6).

Other specimens (coll. MNHN): Maillao (1), Mayo-Kebbi (1).

Literature records: Gounou-Gaya, Bongor (Roussel & Villiers 1965, as *Echis carinatus*), Maillao, Mayo-Kebbi (Hughes 1976, as *Echis ocellatus*), Baïbokoum, Bitanda, Fiengbac, Goulmounbass, Laobida, Yambatchingsou, Zamagouin (Trape 2018).

Remark: This recently described species of the *Echis ocellatus* complex is currently known from Nigeria, Cameroon, Chad, Central African Republic and Sudan (Trape 2018, Trape unpublished).

DISCUSSION

The two most important previous collections of snakes from Chad covered both Sudanese (Roussel & Villiers 1965) and Sahelian (Graber 1966) areas of the country. When adding museum specimens mentioned in works

on certain genera or species, or on the snake fauna of the Saharan part of the country, the number of snakes from Chad mentioned in the literature totaled about 700 specimens belonging to 56 species. We deleted ten of these species (*Tricheilostoma bicolor*, *Boaedon lineatus*, *Boaedon fuliginosus*, *Grayia tholloni*, *Lycophidion irroratum*, *Psammophis schokari*, *Psammophis sibilans*, *Psammophis phillipsi*, *Naja melanoleuca* and *Echis ocellatus*) and reattributed the corresponding specimens to the following species: *Tricheilostoma sundewalli*, *Boaedon longilineatus*, *Boaedon subflavus*, *Grayia smithii*, *Lycophidion semicinctum*, *Psammophis aegyptius*, *Psammophis rukwae*, *Naja subfulva* and *Echis romani*. Among the 1,512 specimens we collected, 66 species were represented, including 27 species that have not been reported before from Chad: *Letheobia weildholzi*, *Myriopholis occipitalis*, *Tricheilostoma sundewalli*, *Crotaphopeltis hippocrepis*, *Dasypeltis sahelensis*, *Natriciteres olivacea*, *Platycephalus florulentus*, *Telescopus tripolitanus*, *Aparallactus lunulatus nigrocollaris*, *Atractaspis dahomeyensis*, *Atractaspis micropholis*, *Boaedon longilineatus*, *Boaedon parolineatus*, *Boaedon perisilvestris*, *Boaedon subflavus*, *Lycophidion* aff. *capense*, *Malpolon moilensis*, *Micrelaps vaillanti*, *Prosymna ambigua*, *Prosymna greigerti*, *Psammophis afroccidentalis*, *Psammophis elegans*, *Psammophis mossambicus*, *Psammophis sudanensis*, *Rhamphiophis rostratus*, *Echis romani*, and *Naja savannula*. In addition, we found in the MNHN collection one specimen of *Spalerosophis diadema cliffordi*, another species not reported before from Chad. Currently, 80 snake species are known from Chad.

As expected, the richest snake fauna was observed in the southern part of the country (07°30'N / 09°00'N) where vegetation is Sudano-Congolese with annual rainfall reaching 1,100–1,300 mm and where 44 species were collected and one additional species is known (Table 3). In a radius of approximately 20 km around Baïbokoum (average rains 1,200 mm according to Mahé et al. [2012]), villagers collected within ten days a total of 505 specimens belonging to 40 species, one of the richest snake fauna for an African savanna area (Fig 8). At Bandafassi in southeastern Senegal (average rains: 1,100 mm) and Mamoroubougou in southern Mali (average rains: 1,000 mm), two Sudan savanna area where 1,282 and 1,064 snakes were collected, 35 and 36 species were represented, respectively (Trape & Mané 2004, 2017).

The most abundant species south of 09°00'N, each one representing at least 5% of the snakes collected, were *Echis romani*, *Boaedon subflavus*, *Psammophis mossambicus*, *Rhamphiophis oxyrhynchus*, *Boaedon parolineatus* and *Psammophis rukwae*. The most remarkable species were *Prosymna ambigua* and *Boaedon perisilvestris* (northernmost limit of these wet Congolese savanna species), *Atractaspis dahomeyensis* and *Naja savannula* (easternmost limit of these West African sa-

vanna species), and *Letheobia weildholzi* and *Myriopholis occipitalis* (rare new species). At Baïbokoum the most abundant species was the deadly viper *Echis romani* which represented 31% of the snakes collected. The number and proportion of specimens of *E. romani* could have been even higher since after a few days we asked the villagers to stop collecting this species. Interestingly, *E. romani* was found only in southwestern Chad and its eastern limit in Chad and Central African Republic is approximately 17°E (Chirio & Ineich 2006, Trape 2018). In Chad this limit corresponds to the seasonally flooded plains of the Logone and Chari rivers system. However, eastward *E. romani* is also widely distributed in the Kordofan province of Sudan (T. Mazuch, personal communication, 2019).

Between 09°00'N and 11°00'N, an area of Sudan savanna, a total of 36 species were collected and eleven additional species are known (Table 3). The most abundant species were *Psammophis lineatus*, *Psammophis sudanensis*, *Psammophis rukwae*, *Boaedon subflavus*, *Echis romani* and *Crotaphopeltis hotamboeia*. The most remarkable species was *Micrelaps vaillanti*, a species previously known only from East Africa and Sudan.

Between 11°00'N and 15°00'N the climate and vegetation are typically Sahelian. A total of 31 species were collected and ten additional species are known (Table 3). The most abundant species were *Psammophis sudanensis*, *Psammophis rukwae*, *Crotaphopeltis hotamboeia*, *Atractaspis watsoni*, *Boaedon subflavus* and *Echis leucogaster*. The abundance of *Crotaphopeltis hotamboeia* was associated to the seasonally flooded areas of the Salamat province where *Crotaphopeltis hippocrepis*, *Crotaphopeltis degeni* and *Causus resimus* – three other amphibian eaters – were also common. Interesting species were *Rhamphiophis rostratus*, *Platycephalus florulentus*, *Psammophis elegans univittatus*, *Atractaspis micropholis* and *Natriciteres olivacea*, which all present important range extensions.

North of 15°00'N the climate and vegetation are Sahelo-Saharan or Saharan. Our investigations were limited and we collected or observed only four of the 13 species that are known in this area where little data is available (Trape 2015). The most common species is *Echis leucogaster* which occurs both in Ouaddai, Ennedi and Tibesti. *Cerastes cerastes* is also a common species. Probably additional species, both Sahelian and Saharan, occur in northern Ouaddai which has never been investigated.

Bauer et al. (2017) recently reviewed the reptile fauna of Libya. In the two Saharan provinces of Libya closest from Chad (Murzuq and Kufrah), nine species of snakes have been reported, including six species also known from northern Chad (*Platycephalus saharicus*, *Spalerosophis diadema cliffordi*, *Malpolon moilensis*, *Psammophis aegyptius*, *Cerastes cerastes* and *Cerastes vipera*), one palearctic species absent from Chad (*Malpolon insignitus*), one species probably present in Chad but not col-

Table 3. Latitudinal distribution of snakes in Chad (our study, 1,512 specimens collected). The 14 species not collected during our study are indicated by a black square (■) with the number of MNHN or literature specimens in brackets. Black triangle (▲) indicates latitudinal occurrence of literature or MNHN specimens when not present at the same latitude in our collection. Latitudes of northernmost records are based on whole data.

* Additional number of species when including literature data and MNHN collection are mentioned in parentheses.

Species	7°N	8°N	9°N	10°N	11°N	12°N	13°N	14°N	≥15°N	Total	Northernmost record in Chad
<i>Platyceps saharicus</i>	0	0	0	0	0	0	0	0	■(3)	■(3)	21°48'N
<i>Cerastes cerastes</i>	0	0	0	0	0	0	0	▲	3	3	21°48'N
<i>Psammophis aegyptius</i>	0	0	0	0	0	■(1)	■(2)	■(1)	■(1)	■(5)	21°34'N
<i>Echis leucogaster</i>	0	0	0	0	4	20	9	4	3	40	21°30'N
<i>Cerastes vipera</i>	0	0	0	0	0	0	0	0	■(2)	■(2)	21°20'N
<i>Myriopholis lanzai</i>	0	0	0	0	0	0	0	0	■(1)	■(1)	17°55'N
<i>Malpolon moilensis</i>	0	0	0	0	0	0	0	0	2	2	17°32'N
<i>Naja nubiae</i>	0	0	0	0	0	0	0	0	■(3)	■(3)	17°30'N
<i>Telescopus obtusus</i>	0	0	0	0	0	0	0	0	■(1)	■(1)	17°12'N
<i>Eryx colubrinus</i>	0	0	0	0	0	4	11	▲	▲	15	16°32'N
<i>Bitis arietans</i>	3	2	▲	1	▲	▲	2	0	2	10	15°57'N
<i>Psammophis rukwae</i>	30	0	7	21	46	39	17	0	▲	160	15°48'N
<i>Spalerosophis diadema</i>	0	0	0	0	0	0	0	0	■(1)	■(1)	15°22'N
<i>Eryx muelleri</i>	0	0	▲	▲	0	9	▲	▲	0	9	14°30'N
<i>Psammophis afroccidentalis</i>	0	0	0	0	0	0	0	1	0	1	14°08'N
<i>Psammophis elegans</i>	6	0	0	7	1	0	0	2	0	16	14°08'N
<i>Naja haje</i>	3	4	▲	3	0	1	8	3	0	22	14°08'N
<i>Platyceps florulentus</i>	0	0	0	0	0	0	5	1	0	6	14°02'N
<i>Atractaspis micropholis</i>	0	0	0	0	0	0	1	1	0	2	14°02'N
<i>Psammophis sudanensis</i>	16	10	4	30	60	21	31	4	0	176	14°02'N
<i>Boaedon subflavus</i>	60	8	9	16	9	12	11	0	0	125	13°54'N
<i>Naja nigricollis</i>	8	9	5	5	0	▲	▲	0	0	27	13°50'N
<i>Meizodon semiornatus</i>	0	0	0	0	0	1	▲	0	0	1	13°50'N
<i>Lycophidion taylori</i>	0	0	0	0	1	1	0	0	0	2	13°50'N
<i>Prosymna collaris</i>	0	1	4	0	1	4	▲	0	0	10	13°50'N
<i>Atractaspis watsoni</i>	0	0	7	5	26	7	11	0	0	56	13°30'N
<i>Rhamphiophis rostratus</i>	0	0	0	0	0	0	1	0	0	1	13°30'N
<i>Myriopholis boueti</i>	0	0	0	3	1	4	1	0	0	9	13°30'N
<i>Python sebae</i>	0	0	1	0	4	0	2	0	0	7	13°30'N
<i>Telescopus tripolitanus</i>	0	0	0	9	0	1	2	0	0	12	13°30'N
<i>Dasypeltis gansi</i>	8	2	4	0	0	0	▲	0	0	14	13°28'N
<i>Causus resimus</i>	0	0	2	1	20	5	▲	0	0	28	13°28'N
<i>Natriciteres olivacea</i>	0	0	0	0	0	0	1	0	0	1	13°26'N
<i>Naja subfulva</i>	0	1	▲	0	0	0	1	0	0	2	13°26'N
<i>Crotaphopeltis hotamboeia</i>	18	7	3	17	56	21	▲	0	0	122	13°13'N
<i>Dasypeltis sahelensis</i>	0	0	0	2	2	3	0	0	0	7	12°40'N
<i>Afrotyphlops punctatus</i>	9	2	1	3	0	0	0	0	0	15	12°40'N
<i>Boaedon longilineatus</i>	0	0	3	4	7	4	0	0	0	18	12°33'N
<i>Micrelaps vaillanti</i>	0	0	0	5	0	2	0	0	0	7	12°07'N
<i>Afrotyphlops lineolatus</i>	0	0	0	0	■(2)	■(2)	0	0	0	■(4)	12°06'N
<i>Crotaphopeltis degeni</i>	0	0	2	13	7	1	0	0	0	23	12°06'N
<i>Scaphiophis albopunctatus</i>	6	0	3	2	0	▲	0	0	0	11	12°06'N
<i>Hemirhagerhis nototaenia</i>	1	0	▲	1	0	0	0	0	0	2	12°06'N
<i>Psammophis lineatus</i>	15	2	5	42	0	▲	0	0	0	64	12°06'N
<i>Causus maculatus</i>	8	1	1	8	▲	▲	0	0	0	18	12°06'N
<i>Philothamnus irregularis</i>	18	0	4	0	0	▲	0	0	0	22	12°06'N

Table 3. continued.

<i>Rhamphiophis oxyrhynchus</i>	21	15	4	11	3	1	0	0	0	55	12°06'N
<i>Prosymna greigerti</i>	4	2	0	1	6	4	0	0	0	17	12°03'N
<i>Philothamnus</i> aff. <i>semivariiegatus</i>	1	2	0	0	0	0	0	0	0	3	11°35'N
<i>Echis romani</i>	127	6	21	1	▲	0	0	0	0	155	11°35'N
<i>Crotaphopeltis hippocrepis</i>	2	1	0	0	11	0	0	0	0	14	11°01'N
<i>Psammophis praeornatus</i>	0	0	■(1)	■(1)	0	0	0	0	0	■(2)	10°53'N
<i>Lycophidion</i> aff. <i>capense</i>	0	0	0	3	0	0	0	0	0	3	10°41'N
<i>Myriopholis adleri</i>	0	0	0	■(3)	0	0	0	0	0	■(3)	10°16'N
<i>Python regius</i>	5	0	1	▲	0	0	0	0	0	6	10°16'N
<i>Amblyodipsas unicolor</i>	2	1	1	0	0	0	0	0	0	4	09°47'N
<i>Meizodon coronatus</i>	3	0	1	0	0	0	0	0	0	4	09°37'N
<i>Tricheilostoma sundewalli</i>	1	0	▲	0	0	0	0	0	0	1	09°37'N
<i>Dasypeltis confusa</i>	2	0	▲	0	0	0	0	0	0	2	09°37'N
<i>Dispholidus typus</i>	5	1	▲	0	0	0	0	0	0	6	09°37'N
<i>Grayia smithii</i>	0	0	■(2)	0	0	0	0	0	0	■(2)	09°37'N
<i>Telescopus variegatus</i>	3	1	10	0	0	0	0	0	0	14	09°37'N
<i>Limaformosa crossi</i>	10	1	1	0	0	0	0	0	0	12	09°37'N
<i>Lycophidion semicinctum</i>	8	11	1	0	0	0	0	0	0	20	09°37'N
<i>Elapsoidea semiannulata</i>	14	2	▲	0	0	0	0	0	0	16	09°37'N
<i>Meizodon regularis</i>	0	0	■(1)	0	0	0	0	0	0	■(1)	09°29'N
<i>Psammophis mossambicus</i>	41	14	6	0	0	0	0	0	0	61	09°13'N
<i>Boaedon parolineatus</i>	31	3	0	0	0	0	0	0	0	34	09°12'N
<i>Atractaspis aterrima</i>	0	0	■(1)	0	0	0	0	0	0	■(1)	09°08'N
<i>Philothamnus bequaerti</i>	1	1	▲	0	0	0	0	0	0	2	09°08'N
<i>Philothamnus hughesi</i>	0	■(1)	0	0	0	0	0	0	0	■(1)	08°30'N (?)
<i>Myriopholis occipitalis</i>	0	1	0	0	0	0	0	0	0	1	08°20'N
<i>Prosymna ambigua</i>	0	1	0	0	0	0	0	0	0	1	08°20'N
<i>Elapsoidea laticincta</i>	2	0	0	0	0	0	0	0	0	2	07°55'N
<i>Letheobia weildholzi</i>	1	0	0	0	0	0	0	0	0	1	07°44'N
<i>Aparallactus lunulatus</i>	4	0	0	0	0	0	0	0	0	4	07°44'N
<i>Atractaspis dahomeyensis</i>	4	0	0	0	0	0	0	0	0	4	07°44'N
<i>Boaedon perisilvestris</i>	2	0	0	0	0	0	0	0	0	2	07°44'N
<i>Gonionotophis granti</i>	1	0	0	0	0	0	0	0	0	1	07°44'N
<i>Naja savannula</i>	1	0	0	0	0	0	0	0	0	1	07°35'N
Number of specimens	505	112	111	214	265	165	114	16	10	1512	
Number of species	40	28	26	25	18	21	16	7	3	66	
Cumulated number of species by ecoregion*		44 (+1)		36 (+12)				31 (+10)	4 (+9)	66 (+14)	

lected until now (*Lytorhynchus diadema*) and one species with doubtfull mentions from Chad and southeastern Libya (*Psammophis schokari*). Interestingly, no *Echis* species has been reported from Murzuk and Kufrah districts (Bauer et al. 2017).

Compared to Niger (51 species) and Mali (65 species) (Trape & Mané 2015, 2017), two other large African countries extending both in the Sahara, Sahel and Sudan savanna, the snake fauna of Chad appears more diversified. Of 103 taxa (101 species and two additional subspecies) known in at least one of these three countries,

only 45 (43.7 %) were reported both from Mali and Chad (Table 4). Among the other taxa, 28 taxa known in Chad but not in Mali are typical Central African species or East African “invaders” (Hughes 1985), 16 taxa known in Mali but not in Chad are typical West African species, and 15 taxa, including two taxa reported only from Niger (*Myriopholis cairi* and *Litorhynchus diadema*), were not collected in Chad (three taxa) or in Mali (14 taxa) probably or possibly due to unsufficient sampling.

Compared to Cameroon (Chirio & Lebreton 2007), all species known from this country north of 08°N were also

Table 4. Comparison of the snake fauna of Chad, Niger and Mali. Data for Niger and Mali are from Trape & Mané (2015, 2017).

Species	Chad	Niger	Mali	Species	Chad	Niger	Mali
<i>Afrotyphlops lineolatus</i>	X	X	X	<i>Telescopus obtusus</i>	X		
<i>Afrotyphlops punctatus</i>	X	X	X	<i>Telescopus tripolitanus</i>	X	X	X
<i>Letheobia weildholzi</i>	X			<i>Telescopus variegatus</i>	X		X
<i>Myriopholis adleri</i>	X	X	X	<i>Amblyodipsas unicolor</i>	X		X
<i>Myriopholis algeriensis</i>		X	X	<i>Aparallactus lunulatus nigrocollaris</i>	X		
<i>Myriopholis boueti</i>	X	X	X	<i>Atractaspis aterrima</i>	X		X
<i>Myriopholis cairi</i>		X		<i>Atractaspis dahomeyensis</i>	X		X
<i>Myriopholis lanzai</i>	X			<i>Atractaspis micropholis</i>	X	X	X
<i>Myriopholis occipitalis</i>	X			<i>Atractaspis watsoni</i>	X	X	X
<i>Rhinoguinea magna</i>			X	<i>Boaedon fuliginosus</i>		X	X
<i>Rhinoleptus koniagui</i>			X	<i>Boaedon lineatus</i>		X	X
<i>Tricheilostoma bicolor</i>		X	X	<i>Boaedon longilineatus</i>	X		
<i>Tricheilostoma sundewalli</i>	X			<i>Boaedon paralineatus</i>	X		
<i>Eryx colubrinus</i>	X	X		<i>Boaedon perisilvestris</i>	X		
<i>Eryx muelleri</i>	X	X	X	<i>Boaedon subflavus</i>	X		
<i>Python regius</i>	X	X	X	<i>Gonionotophis granti</i>	X	X	X
<i>Python sebae</i>	X	X	X	<i>Hemirhagerhhis nototaenia</i>	X	X	
<i>Afronatrix anoscopus</i>			X	<i>Limaformosa crossi</i>	X	X	X
<i>Bamanophis dorri</i>			X	<i>Lycophidion aff. capense</i>	X		
<i>Crotaphopeltis degeni</i>	X			<i>Lycophidion albomaculatum</i>			X
<i>Crotaphopeltis hippocrepis</i>	X		X	<i>Lycophidion irroratum</i>			X
<i>Crotaphopeltis hotamboeia</i>	X	X	X	<i>Lycophidion semicinctum</i>	X	X	X
<i>Dasypeltis confusa</i>	X		X	<i>Lycophidion taylori</i>	X		
<i>Dasypeltis gansi</i>	X	X	X	<i>Malpolon moilensis</i>	X	X	X
<i>Dasypeltis latericia</i>			X	<i>Micrelaps vaillanti</i>	X		
<i>Dasypeltis sahelensis</i>	X	X	X	<i>Polemon neuwiedi</i>			X
<i>Dispholidus aff. typus</i>	X		X	<i>Prosymna ambigua</i>	X		
<i>Grayia smithii</i>	X	X	X	<i>Prosymna collaris</i>	X	X	X
<i>Litorhynchus diadema</i>		X		<i>Prosymna greigerti</i>	X		X
<i>Meizodon coronatus</i>	X	X	X	<i>Psammophis aegyptius</i>	X	X	
<i>Meizodon regularis</i>	X			<i>Psammophis afroccidentalis</i>	X	X	X
<i>Meizodon semiornatus tchadensis</i>	X			<i>Psammophis elegans elegans</i>	X	X	X
<i>Natriciteres olivacea</i>	X	X	X	<i>Psammophis elegans univittatus</i>	X	X	
<i>Philothamnus bequaerti</i>	X			<i>Psammophis lineatus</i>	X	X	X
<i>Philothamnus hughesi</i>	X			<i>Psammophis mossambicus</i>	X		
<i>Philothamnus irregularis</i>	X	X	X	<i>Psammophis phillipsi</i>			X
<i>Philothamnus aff. semivariegatus</i>	X	X	X	<i>Psammophis praeornatus gribinguiensis</i>	X		
<i>Platyiceps florulentus</i>	X			<i>Psammophis praeornatus praeornatus</i>		X	X
<i>Scaphiophis albopunctatus</i>	X			<i>Psammophis rukwae</i>	X		
<i>Spalerosophis diadema cliffordi</i>	X	X	X	<i>Psammophis schokari</i>			X

Table 4. Continued.

Species	Chad	Niger	Mali
<i>Psammophis sudanensis</i>	X	X	
<i>Rhamphiophis oxyrhynchus</i>	X	X	X
<i>Rhamphiophis rostratus</i>	X		
<i>Elapsoidea laticincta</i>	X		
<i>Elapsoidea semiannulata moebiusi</i>	X	X	X
<i>Naja haje</i>	X	X	X
<i>Naja katiensis</i>			X
<i>Naja nigricollis</i>	X	X	X
<i>Naja nubiae</i>	X	X	
<i>Naja savannula</i>	X	X	X
<i>Naja senegalensis</i>		X	X
<i>Naja subfulva</i>	X		
<i>Bitis arietans</i>	X	X	X
<i>Causus maculatus</i>	X	X	X
<i>Causus resimus</i>	X		
<i>Cerastes cerastes</i>	X	X	X
<i>Cerastes vipera</i>	X	X	X
<i>Echis jogeri</i>			X
<i>Echis leucogaster</i>	X	X	X
<i>Echis ocellatus</i>		X	X
<i>Echis romani</i>	X		

collected in Chad, with the exception of only three species: *Psammophylax togoensis*, which is rare in West and Central Africa, *Naja katiensis*, a species common in the West African Sudan savanna but reaching its eastern limit in Cameroon near the Nigerian border, and *Philothamnus heterodermus*, a forest species with a single record in Cameroon north of 08°N (Chirio & LeBreton 2007). A fourth species not found in Chad, *Afronatrix anoscopus*, was mapped in error from northern Cameroon by these authors (M. LeBreton, pers. comm.), then by Chipaux & Jackson (2019). Likewise, when excluding Sahelo-Saharan species, most species distributed in Chad are also known from Cameroon, with only four species likely to reach their westernmost limit in central Chad: *Myriopholis occipitalis*, *Micrelaps vaillanti*, *Rhamphiophis rostratus* and *Lycophidion taylori*.

Snakes presenting a high risk of death for humans in case of bite were distributed in all regions of the country and represented 17.7 % of the total number of snakes collected. They belonged to (a) four viperid species: *Echis romani* (10.3 %), *Echis leucogaster* (2.6 %), *Bitis arietans* (0.6 %), and *Cerastes cerastes* (0.2 %), (b) four elapid species: *Naja nigricollis* (1.8 %), *Naja haje* (1.5

%), *Naja subfulva* (0.1 %) and *Naja savannula* (0.1 %), and (c) one colubrid species: *Dispholidus* aff. *typus* (0.4 %). Atractaspids (4.1 %), in particular *Atractaspis watsoni*, were also common and they are known to be occasionally responsible for fatal envenomations (Spawls & Branch 2020). The distribution of *Echis romani* appears limited to the southwest of the country where it is clearly a major medical problem. Several dozens of cases of *Echis romani* bites are hospitalized each year at Baïbokoum. Although antivenoms were provided to district hospitals by the Ministry of Health, until recently they were not adapted to the species of snakes encountered in Chad (they were manufactured in India where non-african snakes were used in their production) and modalities of administration were often unsatisfactory, with insufficient dosage in case of severe envenomation. In Chad as in other countries of tropical Africa there is an urgent need to improve access to effective antivenoms and to train health workers for adequate management of snake-bite.

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APPENDIX I

List of collected specimens, locality, and collection number (IRD Dakar and PNLP N'Djaména)

Afrotyphlops punctatus. **Baïbokoum**: 2051.N, 2151.N, 2258.N, 2259.N, 2261.N, 2296.N, 2303.N, 2304.N, 2305.N; **Bitanda**: 2605.N; **Bon Amdaoud**: 1967.N, 3041.N, 3066.N; **Moundou** (Belaba): 2622.N; **Zamagouin**: 2561.N.

Amblyodipsas unicolor. **Baïbokoum**: 2209.N, 2286.N; **Moïssala**: 2710.N; **Tikem** (Goundwaye): 2555.N.

Aparallactus lunulatus nigrocollaris. **Baïbokoum**: 2158.N, 2178.N, 2366.N, 2403.N.

Atractaspis dahomeyensis. **Baïbokoum**: 2197.N, 2278.N, 2293.N, 2307.N.

Atractaspis micropholis. **Arningmalik**: 1833.N; **Gouroungali**: 1873.N.

Atractaspis watsoni. **Bahar**: 2987.N, 2988.N, 3003.N; **Balani**: 2523.N, 2565.N.; **Bitea**: 1843.N, 1854.N, 1863.N, 1866.N, 2877.N, 2878.N, 2896.N, 2897.N, 2928.N, 2929.N, 2930.N; **Bon Amdaoud**: 3056.N, 3061.N, 3113.N; **Djarat Abounimir**: 1938.N, 3138.N, 3139.N, 3140.N, 3157.N, 3158.N, 3159.N, 3165.N, 3166.N; **Goulmounbass**: 2649.N; **Guirli**: 2921.N; **Hileborno**: 3274.N, 3275.N, 3276.N; **Kadam Digas**: 1822.N, 1823.N, 2826.N, 2827.N, 2830.N, 2836.N, 2837.N, 2841.N, 2845.N, 2854.N, 2856.N, 2858.N, 2859.N, 2863.N; **Kiéké**: 3033.N; **Mahargal**: 2939.N, 2940.N; **Masarma**: 2821.N; **Zamagouin**: 2517.N, 2526.N, 2539.N, 2743.N, 2748.N.

Bitis arietans. **Baïbokoum**: 2052.N, 2372.N, 2422.N; **Bitea**: 2911.N; **Bon Amdaoud**: 3047.N; **Matafo 2**: 2788.N; **Moïssala**: 3277.N, 3278.N.

Boaedon longilineatus. **Bahar**: 2977.N; **Bon Amdaoud**: 3068.N, 3085.N; **Djarat Abounimir**: 1939.N, 3155.N, 3156.N, 3160.N, 3161.N, 3162.N; **Fiengbac**: 2521.N, 2553.N; **Goulmounbass**: 2626.N, 2627.N; **Hileborno**: 2923.N; **Masarma**: 2809.N, 2818.N, 2823.N; **Zamagouin**: 2558.N.

Boaedon parolineatus. **Baïbokoum**: 2012.N, 2015.N, 2016.N, 2018.N, 2028.N, 2029.N, 2069.N, 2074.N, 2081.N, 2089.N, 2094.N, 2111.N, 2113.N, 2117.N, 2138.N, 2153.N, 2155.N, 2159.N, 2160.N, 2162.N, 2164.N, 2184.N, 2194.N, 2206.N, 2208.N, 2217.N, 2243.N, 2311.N, 2315.N, 2338.N, 2505.N; **Bitanda**: 2575.N, 2576.N, 2606.N.

Boaedon perisilvestris. **Baïbokoum**: 2143.N, 2191.N.

Boaedon subflavus. **Bahar**: 1892.N, 2984.N, 2986.N, 3007.N, 3008.N, 3009.N, 3010.N, 3015.N; **Baïbokoum**: 2004.N, 2009.N, 2017.N, 2027.N, 2030.N, 2044.N, 2045.N, 2046.N, 2047.N, 2049.N, 2050.N, 2055.N, 2082.N, 2086.N, 2090.N, 2102.N, 2105.N, 2108.N, 2109.N, 2110.N, 2116.N, 2144.N, 2154.N, 2161.N, 2163.N, 2165.N, 2166.N, 2181.N, 2182.N, 2187.N, 2188.N, 2189.N, 2196.N, 2198.N, 2199.N, 2200.N, 2207.N, 2212.N, 2214.N, 2247.N, 2248.N, 2275.N, 2284.N, 2287.N, 2317.N, 2323.N, 2324.N, 2325.N, 2333.N, 2339.N, 2360.N, 2362.N, 2367.N, 2370.N, 2387.N, 2388.N, 2391.N, 2399.N, 2400.N, 2401.N; **Balani**: 2566.N, 2567.N; **Bitanda**:

2578.N, 2587.N, 2601.N, 2603.N, 2614.N; **Bitea**: 1835.N, 1837.N, 1844.N, 1846.N, 1857.N, 1871.N, 2875.N, 2879.N, 2898.N, 2906.N; **Bon Amdaoud**: 1946.N, 1951.N, 1956.N, 1959.N, 1960.N, 1964.N, 3048.N, 3057.N, 3058.N, 3070.N, 3094.N, 3106.N, 3116.N, 3121.N, 3123.N; **Dourenge**: 2865.N; **Goulmounbass**: 2629.N; **Kadam Digas**: 2773.N, 2829.N, 2833.N, 2839.N, 2848.N, 2849.N, 2850.N, 2857.N, 2864.N; **Laobida**: 2729.N, 2731.N; **Laobida** (Malgandi): 2571.N; **Laobida** (Yamba-Tchangsou): 2518.N; **Mahargal**: 2935.N, 2965.N, 2966.N, 2967.N; **Moundou**: 2618.N, 2623.N; **Moundou** (Belaba): 2624.N; **Tikem**: 2520.N; **Zamagouin**: 2741.N, 2751.N.

Causus maculatus. **Baïbokoum**: 2021.N, 2048.N, 2070.N, 2099.N, 2213.N, 2239.N, 2255.N, 2310.N; **Bitanda**: 2579.N; **Bon Amdaoud**: 3049.N, 3050.N, 3077.N, 3081.N, 3089.N, 3096.N, 3104.N, 3111.N; **Laobida** (Malgandi): 2515.N.

Causus resimus. **Bahar**: 2989.N; **Balani**: 2536.N; **Bon Amdaoud**: 3069.N; **Djarat Abounimir**: 1903.N, 1908.N, 1910.N, 1923.N, 1924.N, 1930.N, 1941.N, 3126.N, 3127.N, 3128.N, 3129.N, 3130.N, 3131.N, 3132.N, 3133.N, 3141.N, 3167.N, 3168.N, 3169.N, 3170.N; **Mahargal**: 1874.N, 1886.N; **N'Djaména Gassi**: 1993.N, 2789.N; **Tikem** (Goundwaye): 2537.N.

Cerastes cerastes. **Faya Largeau**: 2779.N; **Oum Chalouba** (Houk): 3280.N; **Ounianga Sérir**: 2777.N.

Crotaphopeltis degeni. **Djarat Abounimir**: 3142.N, 3143.N, 3144.N, 3145.N, 3146.N, 3163.N, 3164.N; **Fiengbac**: 2564.N; **Goulmounbass**: 2638.N, 2639.N, 2640.N, 2641.N, 2642.N, 2643.N, 2644.N, 2645.N, 2646.N, 2647.N, 2648.N; **Kiéké**: 3032.N, 3039.N; **N'Djaména**: 3281.N; **Tikem**: 2510.N.

Crotaphopeltis hippocrepis. **Baïbokoum**: 2041.N, 2076.N; **Bitanda**: 2590.N; **Djarat Abounimir**: 1901.N, 1905.N, 1906.N, 1907.N, 1909.N, 1917.N, 1920.N, 1925.N, 1926.N, 1931.N, 1940.N.

Crotaphopeltis hotamboeia. **Bahar**: 2991.N, 2992.N, 2993.N, 2994.N, 2995.N, 2996.N, 2997.N, 2998.N, 2999.N, 3000.N, 3001.N, 3002.N, 3004.N, 3005.N, 3006.N, 3011.N, 3012.N, 3013.N; **Baïbokoum**: 2024.N, 2125.N, 2152.N, 2201.N, 2219.N, 2257.N, 2262.N, 2328.N, 2350.N, 2358.N, 2361.N, 2364.N, 2368.N, 2389.N, 2395.N, 2397.N, 2402.N, 2420.N; **Bitanda**: 2592.N, 2593.N, 2615.N; **Bon Amdaoud**: 1953.N, 1954.N, 1961.N, 2760.N, 3055.N, 3062.N, 3073.N, 3098.N, 3114.N, 3124.N; **Djarat Abounimir**: 1915.N, 1935.N, 3147.N, 3148.N, 3229.N, 3230.N, 3231.N, 3232.N, 3233.N, 3234.N, 3235.N, 3236.N, 3237.N, 3238.N, 3239.N, 3240.N, 3241.N, 3242.N, 3243.N, 3244.N, 3245.N, 3246.N, 3247.N, 3248.N, 3249.N, 3250.N, 3251.N, 3252.N, 3253.N, 3254.N, 3255.N, 3256.N, 3257.N, 3258.N, 3259.N, 3260.N, 3261.N, 3262.N, 3263.N, 3264.N, 3265.N, 3266.N, 3267.N, 3268.N, 3269.N, 3270.N, 3271.N, 3272.N; **Goulmounbass**: 2630.N; **Hileborno**: 1898.N; **Kadam Digas**: 2765.N, 2774.N, 2828.N, 2835.N, 2844.N, 2852.N, 2860.N; **Kiéké**: 3023.N, 3024.N, 3026.N, 3029.N, 3031.N, 3035.N; **Laobida**: 2525.N, 2732.N; **Mahargal**: 1875.N, 2964.N, 2968.N; **Moïssala**: 1990.N, 3282.N, 3313.N; **Moundou**: 2621.N.; **Zamagouin**: 2742.N.

Dasypeltis confusa. **Baïbokoum**: 2142.N, 2290.N.

Dasypeltis gansi. Baïbokoum: 2008.N, 2167.N, 2168.N, 2218.N, 2266.N, 2270.N, 2343.N, 2347.N; Laobida: 2548.N, 2549.N; Moïssala: 3283.N, 3284.N; Zamagouin: 2559.N, 2754.N.

Dasypeltis sahelensis. Bon Amdaoud: 3074.N; Goulmounbass: 2650.N; Guirli: 2918.N; Kadam Digas: 1824.N, 1826.N; Mahargal: 2936.N; N'Djaména: 3285.N.

Dispholidus aff. typus. Baïbokoum: 2061.N, 2106.N, 2185.N, 2297.N, 2376.N; Moïssala: 1988.N.

Echis leucogaster. Arningmalik: 1830.N, 1834.N, 2873.N, 2874.N; Bahar: 1896.N, 2990.N; Bitea: 1848.N, 1856.N, 1868.N, 1870.N, 2900.N, 2901.N, 2910.N; Doureng: 1829.N, 2867.N; Fada: 3287.N, 3288.N; Guirli: 2920.N; Kadam Digas: 2766.N, 2776.N, 2846.N, 2853.N; Mahargal: 1877.N, 1883.N, 1885.N, 1887.N, 2958.N, 2959.N, 2960.N, 2961.N, 2962.N, 2963.N; Masarma: 1808.N, 2812.N, 2817.N, 2822.N, 2824.N, 2825.N; Mongo (vicinity): 2508.N; Oum Chalouba: 3286.N.

Echis romani. Baïbokoum: 2011.N, 2013.N, 2014.N, 2026.N, 2034.N, 2035.N, 2038.N, 2039.N, 2042.N, 2043.N, 2057.N, 2078.N, 2079.N, 2080.N, 2085.N, 2096.N, 2100.N, 2101.N, 2115.N, 2124.N, 2126.N, 2127.N, 2128.N, 2133.N, 2134.N, 2135.N, 2139.N, 2140.N, 2141.N, 2157.N, 2169.N, 2176.N, 2190.N, 2230.N, 2268.N, 2272.N, 2318.N, 2322.N, 2331.N, 2332.N, 2334.N, 2335.N, 2336.N, 2337.N, 2351.N, 2354.N, 2357.N, 2373.N, 2423.N, 2424.N, 2425.N, 2426.N, 2427.N, 2428.N, 2429.N, 2430.N, 2431.N, 2432.N, 2433.N, 2434.N, 2435.N, 2436.N, 2437.N, 2438.N, 2439.N, 2440.N, 2441.N, 2442.N, 2443.N, 2444.N, 2445.N, 2446.N, 2447.N, 2448.N, 2449.N, 2450.N, 2451.N, 2452.N, 2453.N, 2454.N, 2455.N, 2456.N, 2457.N, 2458.N, 2464.N, 2465.N, 2466.N, 2467.N, 2468.N, 2469.N, 2470.N, 2471.N, 2472.N, 2473.N, 2474.N, 2475.N, 2476.N, 2477.N, 2478.N, 2479.N, 2480.N, 2481.N, 2482.N, 2483.N, 2484.N, 2485.N, 2486.N, 2487.N, 2488.N, 2489.N, 2490.N, 2491.N, 2492.N, 2493.N, 2494.N, 2495.N, 2496.N, 2497.N, 2498.N, 2499.N, 2500.N, 2501.N, 2502.N, 2503.N, 2504.N, 2506.N, 2507.N; Bitanda: 2573.N, 2583.N, 2586.N, 2595.N, 2609.N, 2610.N; Fiengbac: 2562.N; Goulmounbass: 2628.N; Laobida: 2550.N, 2713.N, 2717.N, 2720.N, 2724.N, 2725.N, 2727.N, 2728.N, 2730.N, 2733.N, 2734.N; Laobida (Berete): 2545.N; Laobida (Yamba-Maloum): 2546.N; Laobida (Yamba-Tchangsou): 2547.N; Zamagouin: 2542.N, 2543.N, 2544.N, 2560.N, 2740.N, 2746.N.

Elapsoidea laticincta. Baïbokoum: 2215.N, 2302.N.

Elapoisea semiannulata moebuisi. Baïbokoum: 2031.N, 2071.N, 2174.N, 2210.N, 2227.N, 2237.N, 2274.N, 2282.N, 2291.N, 2295.N, 2299.N, 2300.N, 2301.N, 2346.N; Moïssala: 1992.N, 3289.N.

Eryx colubrinus. Birim: 2791.N, 2792.N; Bitea: 1838.N, 1845.N; Doureng: 2869.N, 2895.N, 3019.N; Gouroungali: 1872.N; Guirli: 2914.N, 2915.N, 2916.N, 2917.N; Matafo 2: 2784.N; Tarhacha: 2903.N, 2904.N.

Eryx muelleri. Masarma: 1802.N, 1803.N, 1805.N, 1810.N, 2810.N, 2811.N, 2814.N, 2815.N, 2819.

Gonionotophis granti. Baïbokoum: 2195.N.

Hemirhagerhis nototaenia. Baïbokoum: 2065.N; Kiéké: 3030.N.

Letheobia weildhozi. Baïbokoum: 2285.N.

Limaformosa crossi. Baïbokoum: 2007.N, 2060.N, 2084.N, 2107.N, 2249.N, 2319.N, 2352.N, 2353.N, 2359.N, 2385; Bitanda: 2612.N; Zamagouin: 2738.N.

Lycophidion aff. capense. Bon Amdaoud: 3045.N, 3059.N; Kiéké: 3037.N.

Lycophidion semicinctum. Baïbokoum: 2019.N, 2216.N, 2273.N, 2276.N, 2277.N, 2288.N, 2306.N, 2419.N; Bitanda: 2572.N, 2574.N, 2611.N; Laobida: 2735.N; Moïssala: 1980.N, 1982.N, 2709.N, 3292.N, 3293.N, 3294.N, 3295.N, 3312.N.

Lycophidion taylori. Bahar: 2985.N; Hileborno: 2924.N.

Malpolon moilensis Ennedi (17°32'N / 21°29'E): 3309.N; Ouadi Haouach: 3296.N.

Meizodon coronatus. Baïbokoum: 2010.N, 2246.N, 2250.N; Laobida: 2535.N.

Meizodon semiornatus tchadensis. Bahar: 2969.N.

Micrelaps vaillanti. Bon Amdaoud: 3075.N, 3115.N, 3117.N, 3122; Kiéké: 3034.N; Mahargal: 2937.N, 2938.N.

Myriopholis boueti. Bahar: 2932.N, 2933.N, 2934; Béréguet (vicinity of): 2778.N; Bitea: 1865.N; Bon Amdaoud: 1944.N, 3110.N; Guirli: 2919.N; Kiéké: 3020.N.

Myriopholis occipitalis. Moïssala: 3273.N.

Naja haje. Baïbokoum: 2114.N, 2229.N, 2240.N; Birim: 2800.N, 2801.N; Bitanda: 2596.N, 2598.N; Bitea: 2913.N; Bon Amdaoud: 1965.N, 3080.N, 3090.N; Doureng: 1828.N; Mao: 2803.N, 2804.N, 2805.N; Masarma: 1801.N; Matafo 2: 2781.N, 2782.N, 2783.N, 2785.N; Moïssala: 3297.N; Moundou: 2620.N.

Naja nigricollis. Baïbokoum: 2112.N, 2118.N, 2192.N, 2221.N, 2235.N, 2309.N, 2379.N, 2398.N; Bon Amdaoud: 1947.N, 1966.N, 3065.N, 3072.N; Fianga (env): 2509.N; Goulmounbass: 2631.N; Laobida: 2712.N, 2719.N; Moïssala: 1970.N, 1974.N, 1975.N, 1981.N, 1984.N, 1991.N, 2708.N, 3298.N, 3299.N; Zamagouin: 2736.N, 2739.N.

Naja savannula. Baïbokoum (Mboursa): 2281.N.

Naja subfulva. Birim: 2802.N; Bitanda: 2600.N.

Natriciteres olivacea. Birim: 2790.N.

Philothamnus bequaerti. Baïbokoum: 2294.N.; Moïssala: 1972.N.

Philothamnus irregularis. Baïbokoum: 2003.N, 2072.N, 2098.N, 2170.N, 2171.N, 2193.N, 2211.N, 2256.N, 2312.N, 2313.N, 2314.N, 2316.N, 2320.N, 2321.N, 2377.N, 2386.N, 2405.N, 2411.N.; Zamagouin: 2556.N, 2557.N, 2737.N, 2745.N.

Philothamnus semivariiegatus Baïbokoum: 2298.N; Moïssala: 2707.N; Moundou: 2616.N.

Platycephalus florulentus. Arningmalik: 1831.N; Bitea: 1864.N, 2883.N, 2905.N; Doureng: 1827.N, 2868.N.

Prosymna ambigua. Moïssala: 1973.N.

Prosymna collaris. Bahar: 1891.N, 2970.N, 2971.N, 2972.N; Balani: 2538.N, 2568.N; Djarat Abounimir: 3137.N; Fiengbac: 2551.N, 2552.N; Moundou: 2580.N.

Prosymna greigerti. Bahar: 2973.N, 2974.N, 2975.N, 2976.N; Baïbokoum: 2033.N, 2093.N, 2104.N, 2180.N; Bitanda: 2608.N; Bon Amdaoud: 3118.N; Djarat Abounimir: 3134.N, 3135.N, 3136.N; Kadam Digas: 2763.N, 2834.N, 2855.N; Moïssala: 1978.N.

Psammophis afroccidentalis. Mao: 2808.N.

Psammophis elegans elegans. Mao: 2806.N, 2807.N.

Psammophis elegans univittatus. Baïbokoum: 2005.N, 2036.N, 2097.N, 2122.N, 2183.N, 2222.N; Bon Amdaoud: 1955.N, 2761.N, 3082.N, 3083.N, 3092.N, 3100.N, 3125.N; Djarat Abounimir: 1932.N.

Psammophis lineatus. Baïbokoum: 2040.N, 2092.N, 2120.N, 2132.N, 2203.N, 2204.N, 2225.N, 2228.N, 2265.N, 2369.N, 2375.N, 2383.N, 2394.N, 2421.N, 2463.N; Bitanda: 2577.N, 2602.N; Goulmounbass: 2659.N, 2660.N, 2661.N, 2662.N, 2663.N, 2664.N, 2665.N, 2666.N, 2667.N, 2668.N, 2669.N, 2670.N, 2671.N, 2672.N, 2673.N, 2674.N, 2675.N, 2676.N, 2677.N, 2678.N, 2679.N, 2680.N, 2681.N, 2682.N, 2683.N, 2684.N, 2685.N, 2686.N, 2687.N, 2688.N, 2689.N, 2690.N, 2691.N, 2692.N, 2693.N, 2694.N, 2695.N, 2696.N, 2697.N, 2698.N, 2699.N, 2700.N; Léré: 2756.N, 2757.N; Zamagouin: 2534.N, 2747.N, 2752.N.

Psammophis mossambicus. Baïbokoum: 2006.N, 2053.N, 2054.N, 2066.N, 2067.N, 2068.N, 2083.N, 2087.N, 2088.N, 2123.N, 2129.N, 2130.N, 2136.N, 2145.N, 2146.N, 2148.N, 2172.N, 2175.N, 2177.N, 2186.N, 2202.N, 2224.N, 2226.N, 2238.N, 2244.N, 2245.N, 2252.N, 2260.N, 2264.N, 2269.N, 2341.N, 2342.N, 2408.N, 2409.N, 2410.N, 2412.N, 2418.N, 2459.N, 2460.N, 2461.N, 2462.N; Bitanda: 2581; Laobida: 2529.N, 2714.N, 2715.N, 2716.N, 2718.N, 2722.N; Moïssala: 1971.N, 1977.N, 1983.N, 1989.N, 2704.N, 2705.N, 2706.N, 3300.N, 3301.N, 3302.N, 3303.N, 3304.N; Moundou: 2619.N.

Psammophis rukwae. Bahar: 1894.N, 1895.N, 1897.N, 2978.N, 2979.N, 2980.N, 2981.N, 2982.N, 3016.N, 3017.N, 3018.N; Baïbokoum: 2020.N, 2022.N, 2023.N, 2056.N, 2059.N, 2062.N, 2064.N, 2121.N, 2131.N, 2147.N, 2150.N, 2173.N, 2179.N, 2205.N, 2223.N, 2241.N, 2242.N, 2254.N, 2267.N, 2271.N, 2329.N, 2330.N, 2340.N, 2344.N, 2345.N, 2371.N, 2378.N, 2381.N, 2416.N, 2417.N; Birim: 2793.N, 2794.N, 2795.N, 2796.N, 2797.N, 2798.N, 2799.N; Bitea: 1836.N, 1840.N, 1847.N, 1852.N, 1860.N, 2885.N, 2902.N; Bon Amdaoud: 1949.N, 2762.N, 3078.N; Djarat Abounimir: 1914.N, 1916.N, 1919.N, 1928.N, 1937.N, 3151.N, 3152.N, 3153.N, 3154.N, 3201.N, 3202.N, 3203.N, 3204.N, 3205.N, 3206.N, 3207.N, 3208.N, 3209.N, 3210.N, 3211.N, 3212.N, 3213.N, 3214.N, 3215.N, 3216.N, 3217.N, 3218.N, 3219.N,

3220.N, 3221.N, 3222.N, 3223.N, 3224.N, 3225.N, 3226.N, 3227.N, 3228.N; Fiengbac: 2531.N, 2563.N; Goulmounbass: 2651.N, 2652.N, 2653.N, 2654.N, 2655.N, 2656.N, 2657.N, 2658.N; Gouroungali: 2926.N; Hileborno: 1899.N, 1900.N; Kadam Digas: 2764.N, 2831.N, 2832.N, 2838.N, 2851.N; Kiéké: 1942.N, 1943.N, 2758.N, 2759.N, 3021.N, 3022.N, 3025.N, 3027.N, 3038.N, 3040.N; Mahargal: 1878.N, 1881.N, 1888.N, 2945.N, 2946.N, 2947.N, 2948.N, 2949.N, 2950.N, 2951.N, 2952.N; Masarma: 1806.N, 1807.N, 1809.N, 1812.N, 1813.N, 2813.N, 2816.N, 2820.N; Matafo 2: 2786.N, 2787.N; Mataya: 1815.N, 1816.N; N'Djaména (Farcha): 1997.N, 1998.N, 1999.N, 2000.N; N'Djaména (Gassi): 1994.N, 1995.N, 1996.N, 2001.N, 2002.N; Tikem (Goundwaye): 2554.N; Zamagouin: 2522.N, 2744.N, 2749.N, 2753.N.

Psammophis sudanensis. Arningmalik: 1832.N, 2870.N, 2871.N, 2872.N; Bahar: 1893.N, 3014.N; Baïbokoum: 2149.N, 2156.N, 2231.N, 2232.N, 2234.N, 2280.N, 2283.N, 2289.N, 2292.N, 2308.N, 2365.N, 2380.N, 2392.N, 2393.N, 2396.N, 2404.N; Balani: 2527.N; Bitea: 1839.N, 1841.N, 1842.N, 1849.N, 1850.N, 1851.N, 1853.N, 1855.N, 1858.N, 1859.N, 1862.N, 1869.N, 2876.N, 2880.N, 2884.N, 2886.N, 2887.N, 2888.N, 2889.N, 2890.N, 2891.N, 2892.N, 2893.N, 2894.N, 2899.N, 2907.N, 2908.N, 2909.N, 2912.N, 2931.N; Bon Amdaoud: 1945.N, 1948.N, 1950.N, 1952.N, 1957.N, 1958.N, 1962.N, 1969.N, 3044.N, 3046.N, 3053.N, 3054.N, 3060.N, 3071.N, 3076.N, 3079.N, 3087.N, 3091.N, 3093.N, 3095.N, 3105.N, 3107.N, 3108.N, 3109.N, 3112.N; Djarat Abounimir: 1902.N, 1904.N, 1911.N, 1912.N, 1913.N, 1918.N, 1921.N, 1922.N, 1927.N, 1929.N, 1933.N, 1934.N, 1936.N, 3149.N, 3150.N, 3171.N, 3172.N, 3173.N, 3174.N, 3175.N, 3176.N, 3177.N, 3178.N, 3179.N, 3180.N, 3181.N, 3182.N, 3183.N, 3184.N, 3185.N, 3186.N, 3187.N, 3188.N, 3189.N, 3190.N, 3191.N, 3192.N, 3193.N, 3194.N, 3195.N, 3196.N, 3197.N, 3198.N, 3199.N, 3200.N; Doureng: 2866.N; Goulmounbass: 2632.N, 2633.N, 2634.N; Guirli: 2922.N; Hileborno: 2925.N, 3307.N; Kadam Digas: 1818.N, 1819.N, 1820.N, 1821.N, 1825.N, 2769.N, 2770.N, 2771.N, 2772.N, 2840.N, 2842.N, 2843.N, 2862.N; Kiéké: 3028.N, 3036.N; Mahargal: 1876.N, 1879.N, 1880.N, 1882.N, 1884.N, 1889.N, 2941.N, 2942.N, 2943.N, 2944.N, 2953.N, 2954.N, 2955.N, 2956.N, 2957.N; Masarma: 1804.N, 1811.N, 1814.N; Moïssala: 1976.N, 1979.N, 1985.N, 1987.N, 2701.N, 2702.N, 3305.N, 3306.N, 3311; Moundou (Tayé): 2613.N; Zamagouin: 2528.N, 2569.N, 2750.N.

Python regius. Baïbokoum: 2119.N, 2355.N, 2356.N, 2406.N, 2407.N; Laobida (Dobarbian): 2780.N.

Python sebae. Bitea: 1867.N, 2927.N; Hileborno: 3308.N; Kadam Digas: 2775.N, 2861.N; Mataya: 1817.N; Zamagouin: 2530.N.

Rhamphiophis oxyrhynchus. Bahar: 2983.N; Baïbokoum: 2025.N, 2063.N, 2075.N, 2077.N, 2091.N, 2095.N, 2103.N, 2137.N, 2220.N, 2233.N, 2251.N, 2253.N, 2263.N, 2349.N, 2363.N, 2382.N, 2384.N, 2390.N, 2413.N, 2414.N, 2415.N; Bitanda: 2582.N, 2584.N, 2585.N, 2588.N, 2589.N, 2591.N, 2594.N, 2597.N, 2599.N, 2604.N, 2607.N; Bon Amdaoud: 1968.N, 3063.N, 3064.N, 3088.N, 3099.N, 3101.N, 3102.N, 3103.N; Fiengbac: 2511.N; Goulmounbass: 2635.N, 2636.N, 2637.N; Kadam Digas: 2767.N, 2768.N, 2847.N; Laobida: 2711.N, 2723.N; Laobida (Yamba-Tchangsou): 2533.N; Moïssala: 2703.N, 3310.N; Moundou (Belaba): 2617.N, 2625.N.

Rhamphiophis rostratus. **Bitea**: 1861.N.

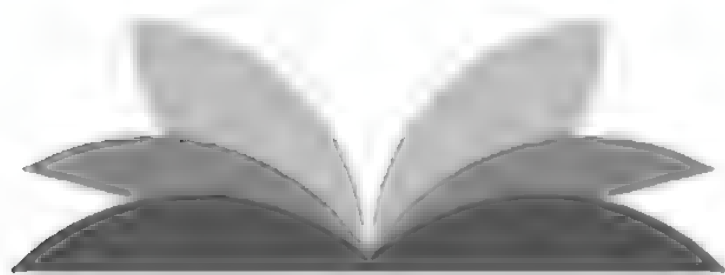
Scaphiophis albopunctatus. **Baïbokoum**: 2037.N, 2236.N, 2279.N, 2326.N, 2327.N, 2348.N; **Bon Amdaoud**: 1963.N, 3084.N; **Laobida** (including Malgandi and Yamba-Tchang-sou): 2721.N, 2514.N, 2519.N.

Telescopus tripolitanus. **Bahar**: 1890.N; **Bitea**: 2881.N, 2882.N; **Bon Amdaoud**: 3042.N, 3043.N, 3051.N, 3052.N, 3067.N, 3086.N, 3097.N, 3119.N, 3120.N.

Telescopus variegatus. **Baïbokoum**: 2032.N, 2058.N, 2374.N; **Laobida**: 2512.N, 2513.N, 2570.N, 2726.N; **Laobida** (Baïbag-la): 2516.N, 2524.N, 2540.N, 2541.N; **Laobida** (Yamba-Maloum): 2532.N; **Moïssala**: 1986 N; **Zamagouin**: 2755.N.

Tricheilostoma sundewalli. **Baïbokoum**: 2073.N.

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Discovery of the second specimen of *Toxicocalamus ernstmayri* O'Shea et al., 2015 (Squamata: Elapidae), the first from Papua Province, Indonesia, with comments on the type locality of *T. grandis* (Boulenger, 1914)

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¹[urn:lsid:zoobank.org:author:DEF1489F-5BCD-4402-96A7-E9263E7BDFD9](https://zoobank.org/author:DEF1489F-5BCD-4402-96A7-E9263E7BDFD9)

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³[urn:lsid:zoobank.org:author:3283F957-6817-4C69-8C31-324D49AF735A](https://zoobank.org/author:3283F957-6817-4C69-8C31-324D49AF735A)

Abstract. Examination of historical specimens from western New Guinea in the Zoologische Staatssammlung Munich, Germany, led to the discovery of only the second specimen of the rarely encountered Star Mountains Worm-eating Snake, *Toxicocalamus ernstmayri*. This specimen is the first record of the species from the Indonesian part of New Guinea, extending its known range northwestward by 150 km. We also question the long-accepted collection locality for another poorly known species, *T. grandis* and document that it was most likely collected further up the Setekwa River at a higher elevation, in habitat more conducive to the ecology of a terrestrial to semi-fossorial genus and in keeping with the known mainland distribution of *Toxicocalamus*.

Keywords. Indonesia, Jayawijaya Range, Sudirman Range, Utekwa River, Setekwa River, rare snake.

INTRODUCTION

Toxicocalamus is an endemic New Guinea genus of secretive, semi-fossorial or terrestrial snakes that occurs throughout the island in both the sovereign state of Papua New Guinea (PNG), which occupies the eastern half of the island, and western New Guinea (WNG), the Indonesian half of New Guinea that includes the provinces Papua and West Papua. These snakes have also been recorded from a number of satellite islands off the coast of PNG, including Seleo (Sandaun Province), Walis and Tarawai (East Sepik Province), and Karkar (Madang Province). *Toxicocalamus* also has an island radiation in the archipelagos of Milne Bay Province, PNG, including six species in the d'Entrecasteaux Archipelago (Good-enough, Fergusson, and Normanby Islands), the Louisiade Archipelago (Misima, Sudest, and Rossel Islands), and on Woodlark Island. Sixteen species are currently recognised, but we expect that this figure will increase considerably due to a recent resurgence of interest in the genus that has already led to the description

of seven species since 2009 (Kraus 2009, 2017, 2020; O'Shea et al. 2015, 2018a).

Toxicocalamus ernstmayri O'Shea et al., 2015 was described from a female holotype (MCZ R-145946) collected by former *kiap*¹ Fred Parker on 23 December 1969 at Wangbin (5.2408° S, 141.2589° E, elev. 1468 m; Fig. 1), a small hamlet near Tabubil in the Star Mountains, North Fly District, Western Province, PNG. It was accessioned into the collection of the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ), as a specimen of *Micropechis ikaheca*² Lesson, 1830, and it remained misidentified until it was examined by the first author during a research visit to the MCZ collection in 2014. With a snout-to-vent length (SVL) of 1.1 m and a total length (TTL) of 1.2 m, the holotype is the largest known specimen of *Toxicocalamus*, a genus which rarely

1 *Kiap* is a word in *tok pisin* (a Papuan creole language), derived from the German for captain and referring to a pre-Independence patrol officer in PNG.

2 The correct spelling is *ikaheca* rather than the commonly used *ikaheka*, according to Lesson's original description.

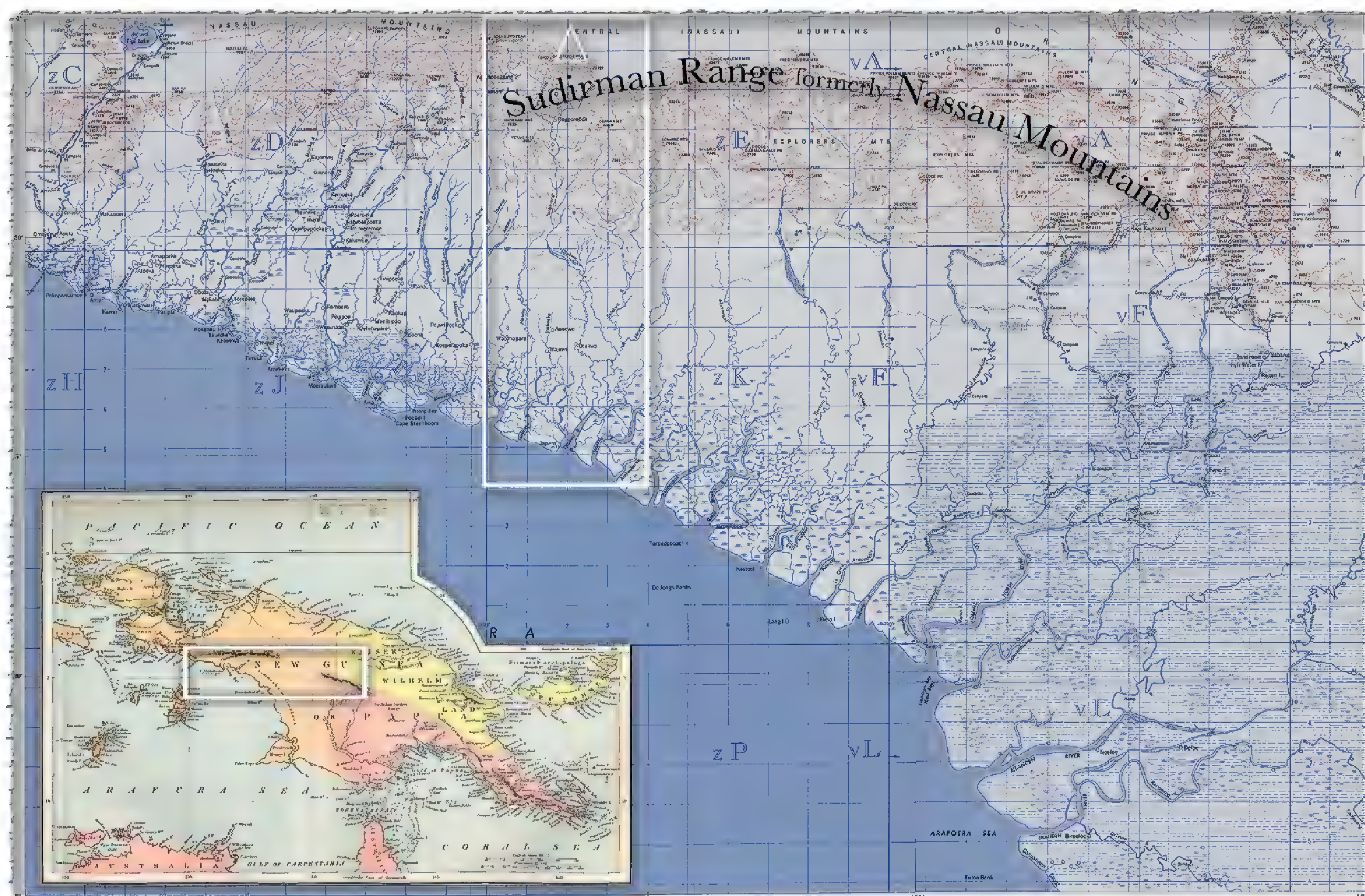


Fig. 1. Note to the reader: This figure comprises a left panel (above) and a right panel at the top of the facing page. Shown is a 1942 map of southwestern New Guinea, including the mountain ranges from which the existing records of *Toxicocalamus ernstmayri* and *T. grandis* were reported. Numbered red circles indicate localities for (1) the holotype of *T. ernstmayri* (MCZ R-145946), (2) the sighting of *T. ernstmayri* at the Ok Tedi Mine (O'Shea et al. 2018b), and (3) the locality where ZSM 55/2015 was collected. The vertical white frame on the main map identifies the location of the Wollaston Expedition of 1912–13, which nearly reached Carstensz Pyramid, now Puncak Jaya (white triangle). The highlighted yellow line is the border between Papua New Guinea to the east and Indonesian West New Guinea to the west. The inset is an 1884 map showing Dutch, German and British boundaries, with the position of the main map, relative to the island of New Guinea, northern Australia, and eastern Indonesia, indicated by the horizontal white frame.

exceeds 600 mm TTL. The only other species of near equal size is *T. grandis* (Boulenger, 1914), whose single specimen is housed in The Natural History Museum, London, United Kingdom (BMNH) and accessioned as BMNH 1946.1.18.34. It was ostensibly collected on the Setekwa River³, southern Papua Province, WNG (Fig. 1) in 1912, and possesses an SVL of 960 mm and a TTL of 1040 mm. A second, live individual of *T. ernstmayri* was identified in 2018 from photographs, which are of an unsexed adult (approximate TTL 850 mm, estimated

from the known size of tire tracks) as it moved slowly and unmolested across an area of active mine workings at the Ok Tedi Mine (5.2150° S, 141.1442° E, elev. 1670 m; Fig. 1) on 9 October 2015 (O'Shea et al. 2018b). The two locations, Wangbin and the Ok Tedi Mine, are only 13.2 km apart and *T. ernstmayri* was presumed to be a localised species found only in the Star Mountains of Western and Sandaun Provinces, PNG.

During a visit to the Zoologische Staatssammlung Munich, Germany (ZSM), the first author examined a small collection of snakes from the mountains of WNG made by the second author in the 1970s. This collection included two specimens of *Toxicocalamus* that had tentatively been identified as *T. grandis*. While the identity of one of these (ZSM 54/2015) still has to be determined, the other (ZSM 55/2015) represents the first known specimen of *T. ernstmayri* from the western half of the island of New Guinea, and we herein document it as such.

³ When dealing with colonial and local place names, it is common that differences in names or spelling exist. Sometimes this is because a colonial power insisted on renaming places that already had local names, as a sign of superiority, oppression, or to honor their leadership, other times honest transcription errors derived from communication problems between the local population and colonial officials crept in, especially when dealing with oral names that were never intended to be written down and which may sound different when spoken by different groups of indigenous people or even individual persons. The names of the Setekwa and Utekwa Rivers in WNG we use here are examples of the latter, and they can also be spelled as Setakwa and Oetakwa.

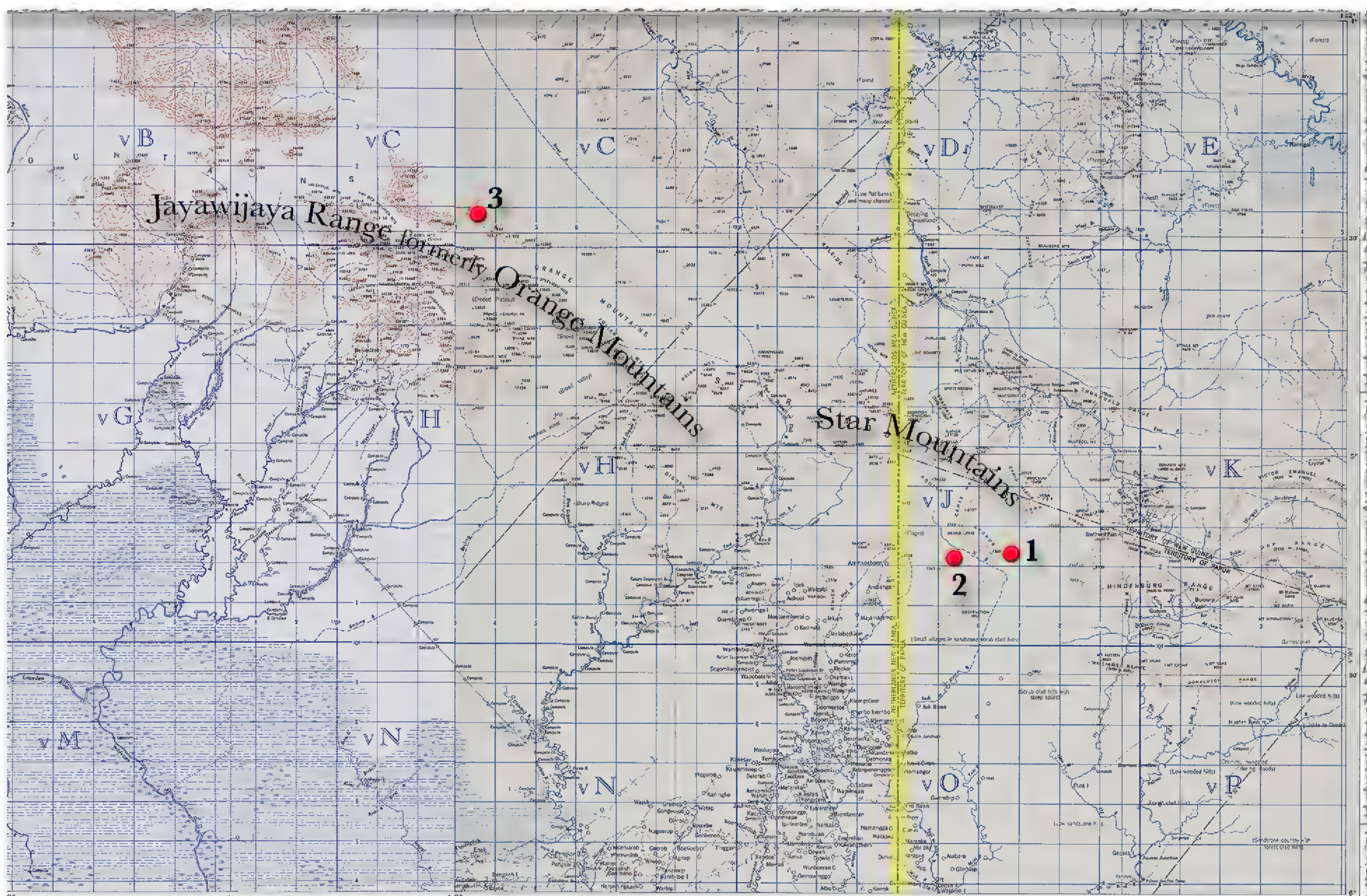


Fig. 1. Continued: right panel.

MATERIALS AND METHODS

Measurements

Our length measurements and our assessment of *Toxicocalamus* scales follow the methods described by O'Shea et al. (2018a). SVL was obtained by running a non-elastic string from the tip of the snout along the ventral medial axis of the body, the string then being placed against a cloth tape-measure taped to a workbench with attention being paid to accuracy of measurement, *fide* Natusch & Shine (2012). Tail length (TL) was easily measured by laying the tail along the tape-measure. TTL is the sum of SVL + TL, and TL as a percentage of TTL was calculated as $TL/TTL \times 100$. Other abbreviations include V (ventrals), SC (subcaudals), SCR (subcaudal ratio, calculated as SC divided by V+SC), SL (supralabials), and IL (infralabials).

Scale counts

Scale counts recorded on the body included dorsals, ventrals, and subcaudals. The dorsal scale rows were counted transversely across the body at three points, one head length posterior to the head, at midbody, and one head length anterior to the cloaca. These counts in

Toxicocalamus are usually 15-15-15, with the exceptions of *T. preussi* (Sternfeld, 1913) with 13-13-13 and *T. longissimus* Boulenger, 1896 with 17-17-17. Dorsal scales of *Toxicocalamus* are smooth without apical pits. Ventral scales, or gastrosteges, were counted beginning with the first broad scale on the anterior part of the body that contacts a scale of the lowest dorsal scale row on both sides, the count then continuing to the scale immediately anterior to the cloacal plate. In *T. pumehanae* O'Shea et al., 2018, this scale is divided into a pair of pre-cloacal scales. The condition of the cloacal plate, entire or paired, is also noted as this has taxonomic implications in *Toxicocalamus*. The condition of the subcaudal scales is also of taxonomic importance since all *Toxicocalamus* except for *T. holopelturus* McDowell, 1969 exhibit paired subcaudals. Subcaudal scales were counted along one side of the tail beginning with the scale immediately posterior to the vent and continuing to the scale immediately anterior to the tail tip; the tail tip was not included in the count. The subcaudal counts of specimens with truncated tails are suffixed with a plus sign (+) indicating the specimen once possessed at least the number of scales counted (e.g., 54+ indicates that the specimen's tail was truncated posterior to scale 54). If present, the shape of the tail tip is recorded as sharply pointed, rounded, or laterally compressed.

Sex and sexual dimorphism

Sex was determined by the examination of the gonads, presence of ova, the presence of everted hemipenes, or the presence of the *retractor penis magnus* muscle. In some species of *Toxicocalamus*, especially the more slender, short-tailed semi-fossorial species *T. preussi* and *T. buergersi* (Sternfeld, 1913), sex can be determined from relative tail length and subcaudal scale counts, with males exhibiting tails more than twice as long as those of females. Females also often exhibit proportionally longer bodies and higher ventral counts than conspecific males.

Head scale patterns

Head scalation provides extremely important clues for species determination in the genus *Toxicocalamus*. Eight of the 16 species, including *T. ernstmayri* and *T. grandis*, exhibit the classic colubrid-elapid dorsal nine-plate arrangement (O'Shea 2005: 12) with distinct and separate pairs of internasals (IN), prefrontals (PF), supraoculars (SO) and parietals (P) with a single central frontal (F). The other eight species exhibit some degree of head scute fusion, either of the internasal and prefrontal or of the prefrontal and preocular (PR), or possesses a pair of large anterior head scutes comprising the fused internasal, prefrontal, and preocular. One species even exhibits fusion of the supraoculars and frontal into a single broad scale across the top of the head. Other important dorsal scales on the head include nasals (N), which may be completely divided by a large naris (nostril) or almost entire with a small countersunk naris in the centre, a rostral (R), preoculars (PR, if not fused with the prefrontals), postoculars (PO) with occasional fusion of the upper PO to the supraocular or the lower PO to a supralabial (SL), and the number and status of the anterior and posterior temporals (AT and PT, respectively). Supralabial counts are provided, and we report which of them contact the orbit (eye) and which is the largest. *Toxicocalamus* is almost unique amongst terrestrial New Guinea elapids in not possessing a temporolabial scale⁴, a diamond-shaped scale protruding downwards between the penultimate and ultimate supralabials. On the ventral side of the head we list the number of infralabials (IL) on either side, noting which contact the anterior and posterior genials (AG and PG, respectively), and whether these scales are themselves in contact at the mental groove or whether the posterior genials are separated by an intergenial (IG). The first pair of ILs is elongate and the only pair that meet at

the mental groove, anterior to the AGs and posterior to the triangular mental (M) at the front of the lower jaw.

Specimen illustrations

Specimens were photographed using the basic methods explained in Kaiser et al. (2018), but with dual photographic set-ups and relatively high-end DSLR equipment to ensure visual clarity in photographs of specimens with very dark, shiny surfaces. All images were uploaded to Aperture 3.6⁵ on a MacBook Pro (OS X Mavericks ver. 10.10). The figures used in this paper were then obtained on a MacPro desktop computer (OS X Sierra ver. 10.12), using Adobe Photoshop CC 2019 and a Wacom Cintiq 13" HD Touch.

RESULTS AND DISCUSSION

Basic morphology and pholidosis

ZSM 55/2015 (Fig. 2A, D) was collected in June 1976 at Dingerkon (4.4508°S, 140.0347°E, elev. 1600 m), Pegunungan Bintang Regency, Papua Province, WNG. This locality is on the Eipomek River in the Jayawijaya (formerly Orange) Range, the mountain range immediately to the west of the Star Mountains (Fig. 1). The specimen was accessioned into the ZSM collection in 2015. ZSM 55/2015 is a female (SVL 765 mm + TL 87 mm = TTL 851 mm). Its scale counts are identical or close to those of the holotype of *T. ernstmayri* (Fig. 2B, E; different values in the holotype provided in parentheses), including a dorsal scale count of 15-15-15; 202 ventrals; a divided cloacal plate; 30 (29) paired subcaudals; SL = 6, with SL3 and SL4 contacting the orbit (Fig. 3A, A', B, B'); IL = 6, with IL1–IL3 in contact with the anterior genials and IL3 and IL4 in contact with the posterior genials; an intergenial scale separating the posterior genials is present (Fig. 4A, A', B, B'); “colubrid-elapid dorsal nine-plate arrangement” of two internasals, two prefrontals, a frontal between two supraoculars, and two parietals on the head; single preocular, in contact with SL2 and SL3; prefrontal and supraocular have broad contact with the nasal; postocular single (paired) in contact with SL4 and SL5, supraocular, and anterior temporal (Fig. 5A, A', B, B', C, C', D, D'); temporal arrangement 1+2 (left: 1+1, right: 1+2). In this listing of scale characteristics, the only differences between ZSM 55/2015 and the holotype of *T. ernstmayri* are one subcaudal scale, the single versus paired postocular condition, and the fusion of the posterior temporals on the left side of the head in the holotype.

⁴ The other terrestrial New Guinea elapid lacking a temporolabial scale is *Pseudonaja*, which is unlikely to be confused with *Toxicocalamus* for numerous reasons, not least its very large eyes. All other terrestrial Papuan elapid genera (*Acanthophis*, *Aspidomorphus*, *Cryptophis*, *Demansia*, *Furina*, *Micropechis*, *Oxyuranus*, and *Pseudechis*), exhibit an obvious temporolabial scale.

⁵ Apple have discontinued and no longer support Aperture. It will also run on OS X High Sierra (10.13) and OS X Mojave (10.14) but not OS X Catalina (10.15). An alternative application is Adobe Lightroom.

The ZSM specimen appears to exhibit a subterminal mouth (an “underbite”), with the lower jaw appearing to extend beyond the upper jaw, combined with an apparent compression of the snout, certainly on the right side (Figs. 5A, A', B, B', 6). The latter is likely an artefact of preservation, such that the snake was stored in a container with its snout pressed against the container's

inner surface. However, the front of the snout does appear to be slightly malformed as seen by the continuation of the prefrontal-internasal suture anteriorly onto the rostral to form a vertical division (Fig. 6). Whether this slight abnormality was the cause or a post-fixation contributory factor to shaping the head as we see it now is open to conjecture.

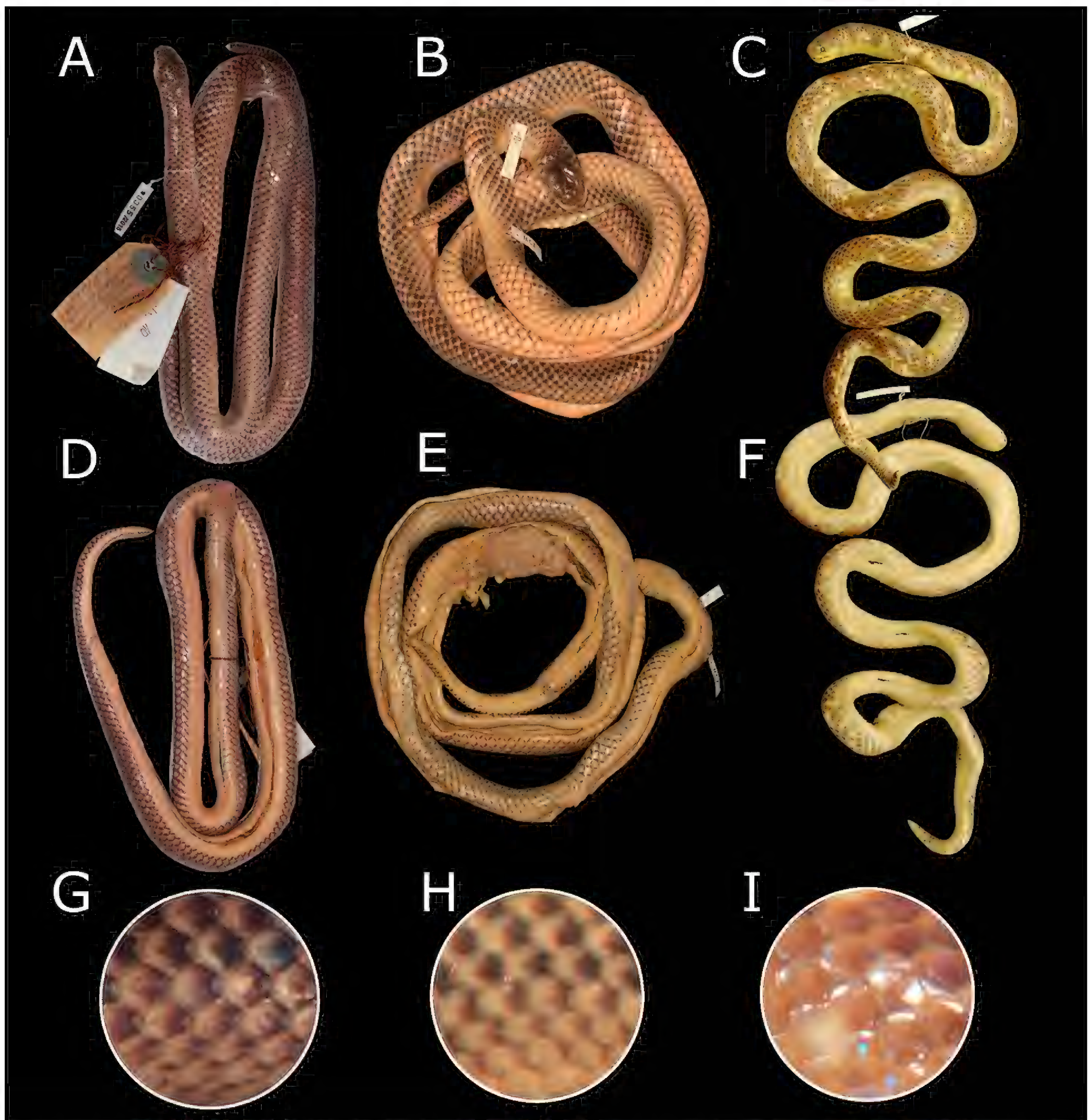


Fig. 2. Whole body views and colour patterning in three specimens of *Toxicocalamus*. Dorsal views include those of (A) ZSM 55/2015; (B) the holotype of *T. ernstmayri* (MCZ R-145946); and (C) the holotype of *T. grandis* (BMNH 1946.1.18.34). Ventral views (D–E) are listed in the same order as the dorsal views. The circular images show closeups of dorsal scale patterns and are provided to illustrate the observed pattern reversal. Whereas the pattern in ZSM 55/2015 (G) and *T. ernstmayri* (H) is characterized by dorsal scales with dark centers and light edging, there is no such prominent patterning in *T. grandis* (I). Images not to scale. Photos by Mark O'Shea.

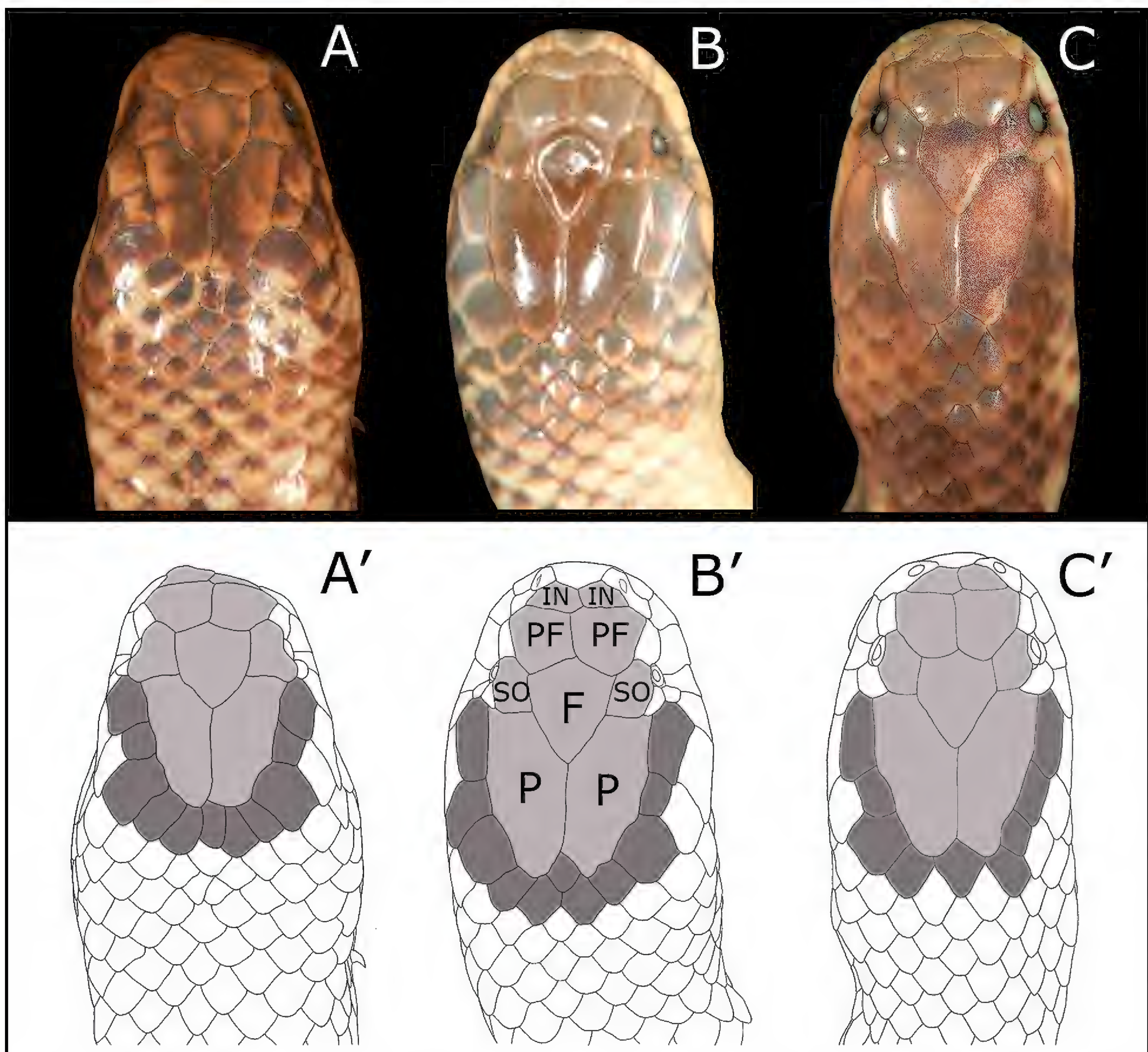


Fig. 3. Dorsal views of the heads of *Toxicocalamus* specimens from New Guinea, presented as both photographic and line-drawing illustrations. The drawing in (B') features the classic colubrid-elapid nine-plate arrangement (light grey), comprising paired internasals (IN), prefrontals (PF), supraoculars (SO), and parietals (P), and single frontal (F), and eleven scales bordering the parietals (mid-grey), including anterior temporals and upper posterior temporals. The drawings in (A') and (C') follow the same pattern. Shown are (A, A') the first West New Guinea specimen of *T. ernstmayri* (ZSM 55/2015), (B, B') the holotype of *T. ernstmayri* (MCZ R-145946), and (C, C') the holotype of *T. grandis* (BMNH 1946.1.18.34). Images not to scale. Photos and line drawings by Mark O'Shea.

Comparisons with *Toxicocalamus grandis*

Differences in scalation between the two extant specimens of *T. ernstmayri* (MCZ R-145946, ZSM 55/2015), and the single known specimen of *T. grandis* (BMNH 1946.1.18.34; Figs. 2C, F, 3; characteristics in parentheses) include broad contact between the preocular and the nasal scales (point contact on the left side and exclusion by contact between SL2 and the prefrontal on the right side; Fig. 5E, E', F, F'), eleven temporal and post-temporal scales bordering the parietals (nine

scales), and SL6 only narrowly separated from the upper posterior temporal (SL6 widely separated by broad contact between the anterior temporal and the lower posterior temporal). The only character in which ZSM 55/2015 agrees with *T. grandis* and not *T. ernstmayri* is the presence of a single postocular where the type of *T. ernstmayri* has a pair of postoculars. Whilst this is perhaps an important difference in the grand scheme of *Toxicocalamus* taxonomy, when weighed against the number of characters in which ZSM 55/2015 agrees with

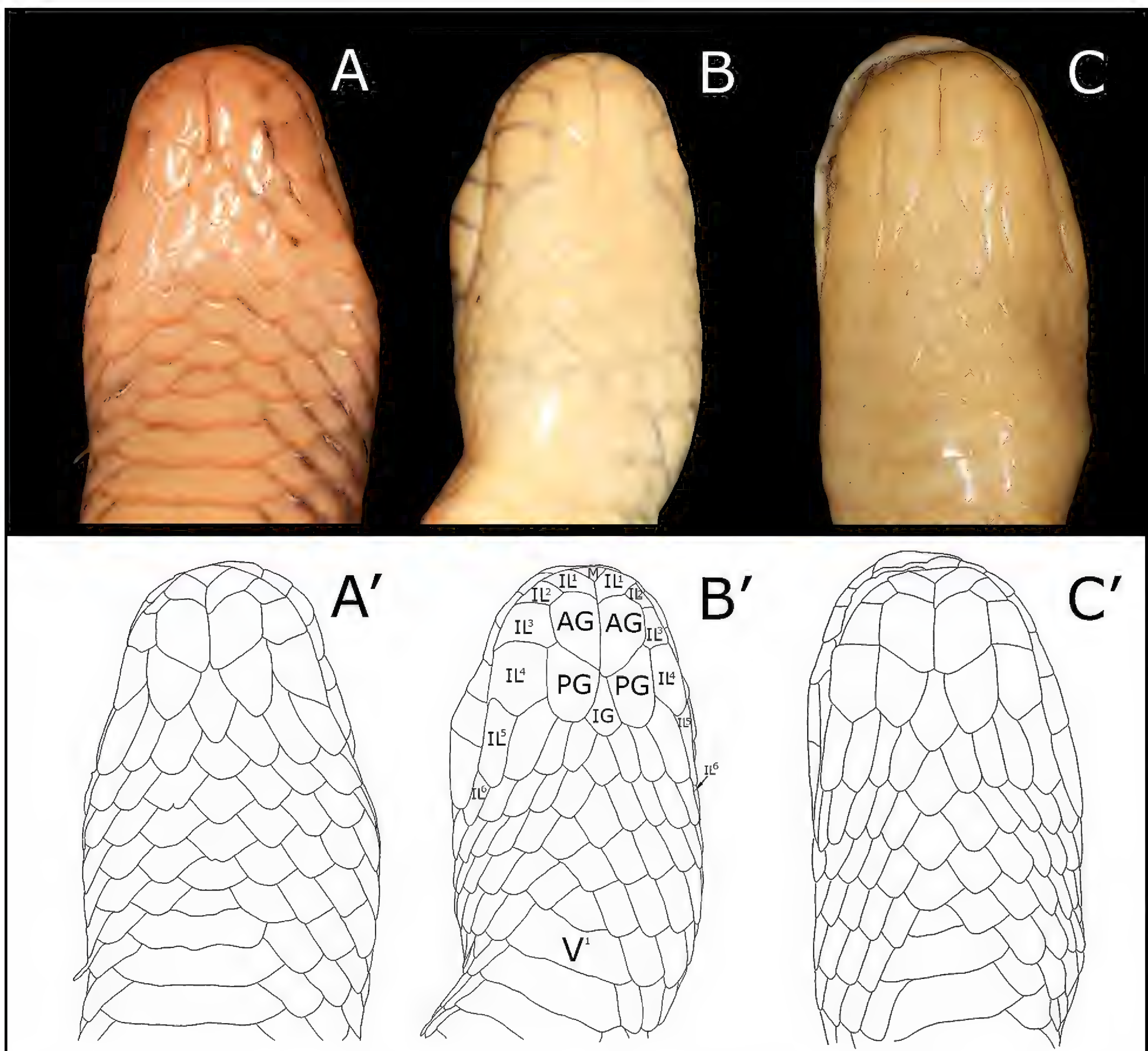


Fig. 4. Ventral views of the heads of *Toxicocalamus* specimens from New Guinea, presented as both photographic and line-drawing illustrations. The drawing in (B') includes scales identified by lettering, including mental (M), numbered infralabials (IL), anterior genials (AG) in contact along the mental groove, posterior genials (PG) separated by an intergenial (IG), and the first gastrostege (V¹). The drawings in (A') and (C') follow the same pattern. Shown are (A, A') the first West New Guinea specimen of *T. ernstmayri* (ZSM 55/2015), (B, B') the holotype of *T. ernstmayri* (MCZ R-145946), and (C, C') the holotype of *T. grandis* (BMNH 1946.1.18.34). Images not to scale. Photos and line drawings by Mark O'Shea.

T. ernstmayri and, given the propensity for scale fusions in the genus, its importance is diminished.

In its colouration, ZSM 55/2015 is remarkably similar to the holotype of *T. ernstmayri*. In the original list of specimens donated to the ZSM both ZSM 54/2015 and ZSM 55/2015 were classified as *T. grandis*, but in BMNH 1946.1.18.34, the only known specimen of that species, the dorsal pattern comprises fairly uniformly coloured scales (Fig. 2I), whereas in both specimens of *T. ernstmayri* (MCZ R-145946, ZSM 55/2015; Fig. 2G,

H, respectively) the pattern is striking, comprising light dorsal scales edged with dark pigmentation.

Natural history and ethnology

The second author participated in a 1976 ethnological and ethnobiological expedition (Fig. 7), conducted by the Museum für Völkerkunde (Ethnological Museum) in Berlin and led by the medical anthropologist

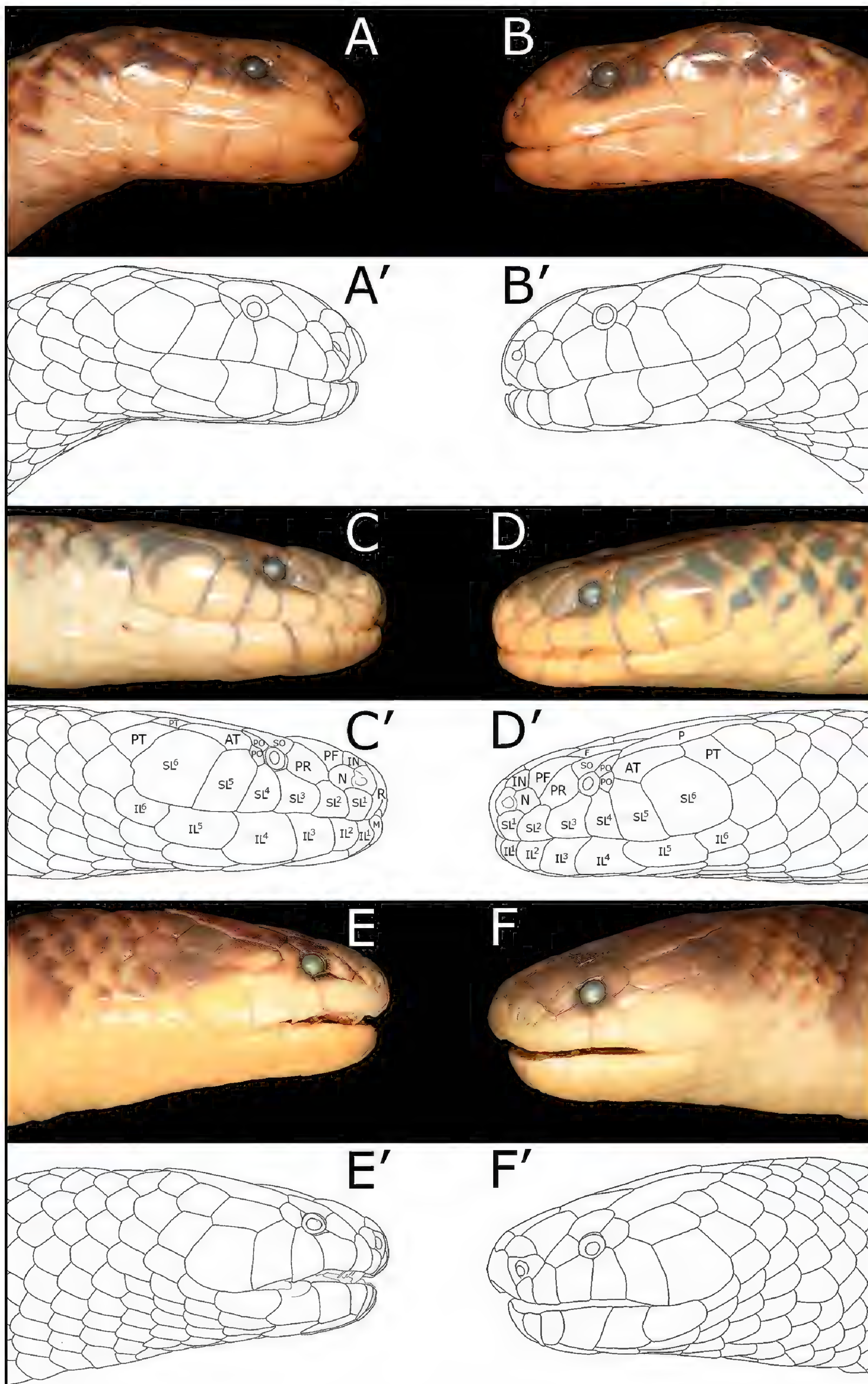


Fig. 5. Lateral views of the heads of *Toxicocalamus* specimens from New Guinea, presented as both photographic and line-drawing illustrations in right and left aspect. The drawings in (C') and (D') include scales identified by lettering, including rostral (R), mental (M), nasals (N), internasals (IN), prefrontals (PF), preoculars (PR), supraoculars (SO), postoculars (PO), anterior temporals (AT), posterior temporals (PT), numbered supraoculars (SL), and numbered infralabials (IL). The drawings in (A', B') and (E', F') follow the same pattern. Shown are the first West New Guinea specimen of *T. ernstmayri* (ZSM 55/2015) in right (A, A') and left (B, B') lateral views, the holotype of *T. ernstmayri* (MCZ R-145946) in right (C, C') and left (D, D') lateral views, and the holotype of *T. grandis* (BMNH 1946.1.18.34) in right (E, E') and left (F, F') lateral views. Images not to scale. Photos and line drawings by Mark O'Shea.

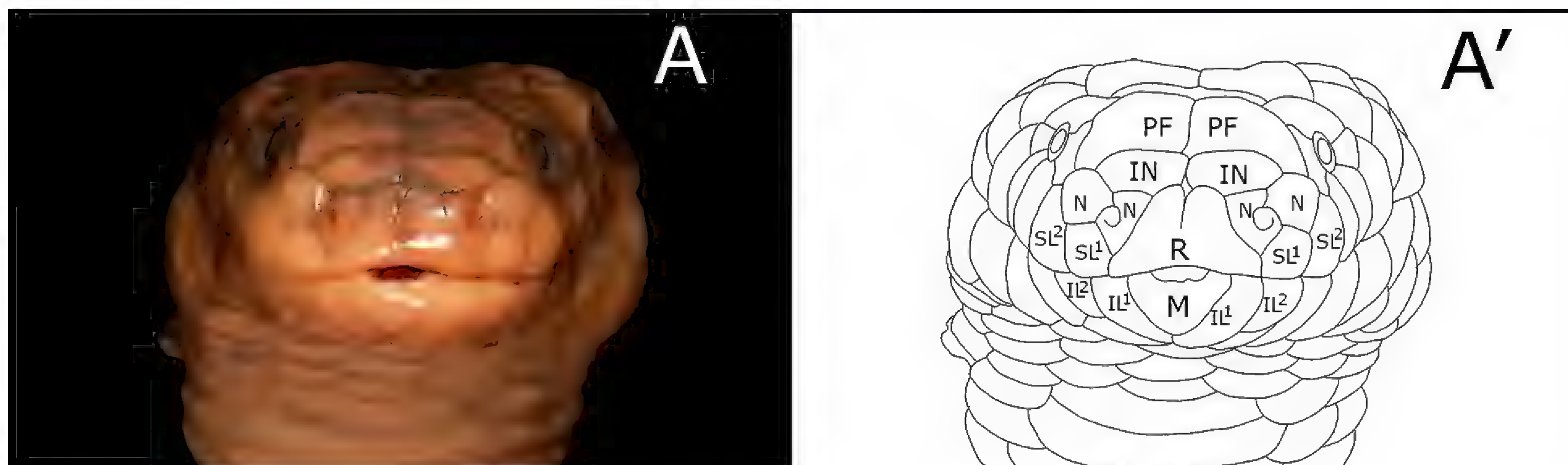


Fig. 6. Frontal view of the head of the first West New Guinea specimen of *T. ernstmayri* (ZSM 55/2015) as a photo (A) and a line drawing (A'), illustrating the deeply scored and deformed rostral (R), divided nasals (N), internasals (IN), prefrontals (PF), supralabials (SL), mental (M), and infralabials (IL). Photo and line drawing by Mark O'Shea.

Wulf Schiefenhövel⁶, to study the Eipo people of the remote Eipomek Valley in central mountainous WNG (Schiefenhövel 1997). We would therefore be remiss if in our account of ZSM 55/2015 we did not include information on how a snake like *T. ernstmayri* is perceived by the indigenous human population. We therefore expand our specific report on this snake to include its relevance to the local residents, who are very much a part of the natural environment in New Guinea.

ZSM 55/2015 was discovered and killed in a village garden (Fig. 8) during daylight hours on 18 June 1976. Snakes of the genus *Toxicocalamus* are believed to be exclusively vermivorous (O'Shea et al. 2015), and they appear to be especially common in highland gardens, possibly because of the abundance of giant earthworms (Annelida: Megascolecidae) in well-turned, irrigated, and composted montane vegetable plots operating for 35,000–60,000 consecutive years (Schiefenhövel 2001). The high density of *Toxicocalamus* in these habitats is supported by the large number (165 specimens = 32% of all known specimens) collected in the heavily populated and intensively farmed Wahgi Valley (Simbu and Jiwaka Provinces, PNG) by Australian *kiap* and herpetologist Fred Parker, Divine Word missionary Father Otto (Shelly) Schellenberger (1914–2007), and other field collectors. That the snake was active during the day is also not unusual, certainly the larger and more terrestrial species (including *T. ernstmayri* and *T. pachysomus*) appear to be diurnally active, as evidenced by the observation of *T. ernstmayri* moving unhurriedly across mine-workings at Ok Tedi in broad daylight (O'Shea et al. 2018b).

The dead snake was delivered to the second author by a Dingerkon villager named Ewinde, who carried it in secrecy and protectively wrapped in three layers of leaves so that other villagers would not see it. The Eipo are apparently frightened by snakes, which they call *kwatema*, but they were especially averse to this species which they call *amau*, considering it highly dangerous⁷ and capable of causing death, and even to look upon it is considered highly undesirable. The second author was warned to be very careful with the dead snake, especially to avoid pricking himself on its sharp tail tip, the keratinized sting-like terminal scale, because that could prove fatal. Thus, the dead snake was positioned on a flat rock and photographed surreptitiously (Fig. 9).

Where is the type locality of *Toxicocalamus grandis*?

The Jayawijaya Range, where ZSM 55/2015 was collected, is adjacent to the Star Mountains of Western Province, where the holotype of *T. ernstmayri* was collected in 1969 and from where the 2018 sighting was documented (Fig. 1). The elevation for these observations ranges from 1468 m at Wangbin, the type locality of *T. ernstmayri*, to 1600 m at Dingerkon, the collection locality of ZSM 55/2015, and to as high as 1670 m at the Ok Tedi Mine. Whereas these specimens and sightings are accurately pinpointed localities, “Launch Camp” on the Setekwa River, where the holotype of *T. grandis* was supposedly collected, has not previously been located with any certainty.

The *T. grandis* holotype (BMNH 1946.1.18.34) was collected by the British explorer Alexander Frederick

⁶ On an earlier ethnological/zoological expedition to New Guinea, the “Papua Expedition 1966” by the Zoological Institute at Ludwigs-Maximilians-Universität Munich (Schultze-Westrum 1968), the expedition leader Thomas Schultze-Westrum was bitten by a Müller's crowned snake (*Aspidomorphus muelleri*). The symptoms and treatment of this snakebite, the only known record of a snakebite from this genus, were documented and published by Schiefenhövel (1969).

⁷ The only toxinological study of *Toxicocalamus* venom was conducted on *T. longissimus* from Woodlark Island, Milne Bay Province, PNG (Calvete et al. 2012). Its venom was found to contain high levels of potentially dangerous 3-finger toxins (3FTx). However, there are no human snakebites due to *Toxicocalamus* on record and the reasons why a vermivorous snake should possess relatively toxic venom are unknown.



Fig. 8. An overgrown garden plot in Dingerkon, West New Guinea, where the recently identified specimen of *Toxicocalamus ernstmayri* (ZSM 55/2015) was collected. The snake was observed in the grass during the day and killed by a villager. Photo by Paul Blum.

“At the mouth of the Oetakwa River we disembarked our baggage into launches. The stores for the Dutch expedition filled nine big boats and my stores another big boat. This string of boats was taken in tow by a steam launch, and like a great snake it wound its way up the river, a full day’s journey. This was the end of navigable water for the steam launch. At this stage, which was called the Launch Stage, I encountered Captain Van der Bie and discussed my arrangements with him. Then two days’ journey further up the river by canoe brought us to what was called the Canoe Stage.” (Meek 1913: 211f)

With Meek’s term “stage” clearly synonymous to a site where expeditions are staged (i.e., a camp or landing stage), it is most likely that Base Camp and Launch Camp are one and the same location, with deep enough water for a motor launch and two days downstream from Canoe Camp (see Wollaston’s map; Fig. 12). This would suggest that the camp from which the expedition originated lay in the very low reaches of the Setekwa River, with an elevation of only 20–30 m. The distribution of *Toxicocalamus* can be loosely summarised as “highland or island” but from the above account it might be assumed that, unlike other mainland New Guinea *Toxicocalamus*,

especially unlike *T. ernstmayri*, *T. grandis* defies that rule and is a southern lowland species.

However, there is a problem with this supposition. In her compilation of her husband’s posthumously published letters and diaries¹¹ Mary Wollaston added the following note:

*“December 8. Up river to ‘Canoe Camp’
At this point in the diary A.F.R. [Sandy Wollaston] makes the following note: ‘On March 9, 1913, coming down the river from Canoe Camp to Base Camp, my canoe upset in a dangerous rapid, so that I was nearly drowned, and I lost the greater part of my baggage, cameras, medicine chest, maps and diaries. Now I have to begin to write over again my diary from December 8, to March 9 – so far as I can remember it. A.F.R.W. March 19, 1913.’”*
(Wollaston 1933: 135)

¹¹ After a life time of living dangerously, which included two expeditions to New Guinea, one to East Africa, participation in the first ever attempt to ascend Mt. Everest with George Mallory (1886–1924), and Royal Naval service in both the Great War and the Russian Civil War, Sandy Wollaston was shot dead by a deranged student at Cambridge University on 3 June 1930 (Wollaston 2003).



Fig. 9. The freshly killed *Toxicocalamus ernstmayri* (ZSM 55/2015), photographed by Paul Blum on 18 June 1976.

Since Wollaston and other naturalist collectors of his era were more interested in birds, beetles, or butterflies than reptiles and amphibians it is likely that they were not as diligent with their recording of specific collection localities for herpetological specimens. Given that Wollaston had lost his diary and been forced to rewrite his journey, from the Setekwa and Utekwa Rivers uphill to an elevation of 4700 m on the slopes of Mt. Carstensz (today Puncak Jaya) and then downhill, weeks after the events had taken place, it is not surprising that no mention was made of an obscure snake.

Furthermore, listing this snake along with a great many other herpetological specimens from the Wollaston Expedition (Boulenger 1914; O'Shea 2013) as originating from the expedition's launching point, Launch Camp, is no different than when the Italian naturalist collector Luigi Maria d'Albertis (1841–1901) listed the collection locality for many of the herpetological specimens collected quite far upriver on the Fly River during his three expeditions (1875–77) as Kataw (or Katau), which was actually his base camp on the south coast, a mooring in the mouth of the Binaturi River, southern Western Province, PNG, and demonstrably not their true collection localities (d'Albertis 1879, 1880; O'Shea & Kaiser 2018). Therefore, without proof that *T. grandis* really does occupy the lower reaches of the Setekwa River and should be aligned ecologically with this

lowland locality, there is a higher probability that it was obtained in an area that is ecologically a better match for a species so similar to the montane *T. ernstmayri*. We consider the likeliest collection area to be much further upstream, on the southern versant of the Sudirman Range, and Wollaston would have collected it on the trip during which he lost his diary, between 8 December 1912 and 9 March 1913.

The two main mountain ranges of Papua Province, WNG, that combined form the Maoke Mountains, formerly Snow Mountains, are the Jayawijaya Range in the east, and the Sudirman Range to the west (Fig. 1). The Jayawijaya Range, formerly known as the Orange Range, extends for 380 km westward from the Star Mountains, which straddle the border between Western and Sandaun Provinces, PNG, and Papua Province, WNG. The highest point in the Jayawijaya Range is Puncak Mandala, formerly Juliana Summit (4760 m). The Sudirman Range, formerly the Nassau Range, is located to the west of the Jayawijaya Range, and it extends the central cordillera a further 692 km westwards, with its highest point at Puncak Jaya, formerly the Carstensz Pyramid (4884 m), a peak so high it was snow-capped until the early 1960s and which still retains some small, but rapidly shrinking, glaciers (Löffler 1982). Both ranges provide a wide range of habitats and exhibit considerable vertebrate diversity and endemism (Allison 2007; Beehler 2007;



Fig. 10. Portraits of (A) Alexander Frederick Richmond “Sandy” Wollaston (1875–1930) photographed in Dutch New Guinea in 1912, and (B) Cecil Boden Kloss (1877–1949) photographed in the field (date and location unknown). Both gentlemen display the attire and character typical of early 20th Century explorers. Note their similarities: both bearded, both bearded, both with belted field kit, both with walking canes (Wollaston always carried his ice-axe), both in cut-off shorts and puttees, both photographed surrounded by field camp debris in an “active pose,” with one leg forward. Images courtesy of (A) Royal Geographical Society and (B) Kevin Tan, National University of Singapore.

Brongersma & Venema 1962). The Jayawijaya and Sudirman Ranges are separated, at an elevation of 1600–1700 m, by the 80 km long and 20 km wide Baliem River Valley, another biodiversity hotspot which was explored by the 3rd Archbold Expedition of 1938–39 (Archbold et al. 1942), and other expeditions have followed subsequently. The Baliem Valley has been called “an important zoogeographic divide and a potential important area of interchange” with regards to mammals (Helgen 2007: 736) and it may also act as a barrier between the two montane herpetofaunas. If *T. ernstmayri* and *T. grandis* are ecologically similar species, large diurnal members of a genus that feeds exclusively on annelids, especially large earthworms, it is possible that they evolved through allopatric speciation, *T. ernstmayri* in the Jayawijaya and Star Mountains, and *T. grandis* in the Sudirman Range. A third relatively large, stocky and poorly known species, *T. pachysomus* Kraus, 2009, is known from its holotype, collected in the Cloudy Mountains at the southeastern end of the Owen Stanley Range. It may also occupy a similarly montane vermivorous niche, albeit at a lower elevation of 715 m.

The discovery of *T. ernstmayri* in the WNG mountains and our sleuthing of historical records to better align *T. grandis* with the ecology expected of a large *Toxicocalamus* lend further support to the ‘highlands

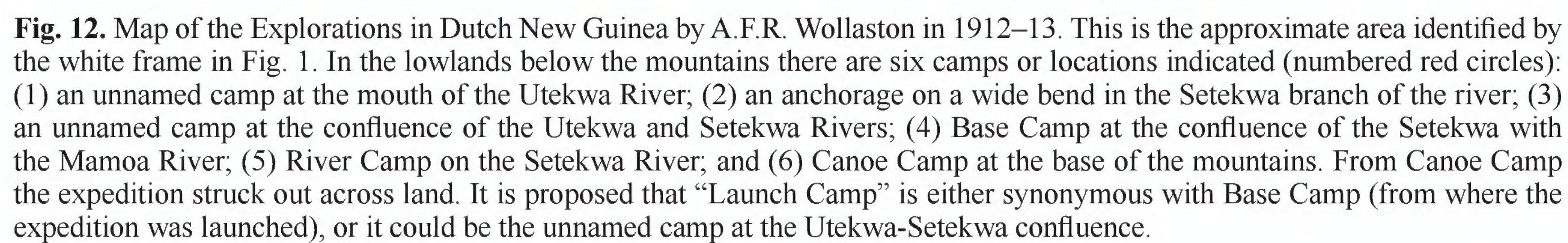
or islands’ biogeographic hypothesis for *Toxicocalamus* diversity. Our findings also provide important insights into how these species may have evolved on the New Guinea mainland, via allopatric speciation, one mountain chain at a time, with the mountain ranges acting like archipelagos in the sky, separating populations with lowland or submontane valleys. The apparent allopatric mountain-derived speciation in *T. ernstmayri* and *T. grandis* means that some of the widely distributed montane species on mainland New Guinea may in reality represent species-complexes, and with this in mind we are currently examining *T. loriae* (Boulenger, 1898), *T. stanleyanus* Boulenger, 1903, and *T. preussi* more closely. *Toxicocalamus* appears to provide a small yet interesting example for the evolution of biodiversity on the world’s largest tropical island.

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Fig. 11. Two photographs from the book *A Naturalist in Cannibal Land* by Albert Stewart Meek (1871–1943). (A) “Dutch Explorers’ Camp, Oetakwa River” shows the lower reaches of the Oetakwa (Utekwa) River. This is either the unnamed camp (Fig. 12: Location 3) at the confluence of the Utekwa and Setekwa Rivers, or Base Camp (Fig. 12: Location 4) at the confluence of the Setekwa and Mamoia Rivers, since the Setekwa is a branch of the Utekwa¹². The river is wide and probably deep enough for a motor launch, and canoes and European skiff-like boats for the journey up-stream are visible in the image. This location could also be the same as Launch Camp, the location Wollaston listed as his purported collection locality for the holotype of *T. grandis*. (B) Meek’s campsite in the Maoke Mountains (historically known as the Snow Mountains) in 1910–11, captioned “My camp under the Snow Mountains, Dutch New Guinea”. Meek is seen sitting on the tree stump. This photograph was taken on Meek’s second venture into Dutch New Guinea, up the Eilanden (Island) River further to the east, so the camp is located in the Jayawijaya (then Orange) Range, the eastern portion of the Maoke Mountains, while the Utekwa and Setekwa Rivers lead to the Sudirman (then Nassau) Range, the western portion of the Maoke Mountains (see Fig. 1).

¹² Meek (1913: 213) referred to Canoe Camp as being on “the right-hand branch of the Oetakwa,” which is the Setekwa River.



hospitality and the generous use of their facilities during his 2015 visit.

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